The effects of food size, pilfering and presence of a human observer on the caching behaviour of the South Island robin (*Petroica australis australis*)

A thesis submitted in partial fulfilment of the requirements for the

Degree

Master of Science in Ecology

University of Canterbury

By Kieran Matthew Tibble

University of Canterbury

2011

Table of Contents

List of Figures

Abstract. – Caching is the behaviour in which an animal stores food for later consumption. The most likely functions of caching are that it ensures food availability when conditions are severe, and it allows storage of energy in a form other than fat. The South Island robin (*Petroica australis australis*) is an endemic songbird that caches food items (such as insects) for later consumption. In this study, I examined caching in robins to address three questions. Firstly, I determined whether caching is related to prey size. I provided robins with mealworm (*Tenebrio molitor*) larva and recorded whether their propensity to cache was determined by prey size. As caching takes energy, robins should be selected to cache only the largest mealworms in which the energy return exceeds the costs of caching. I found that robins were significantly more likely to cache large mealworms while small mealworms were eaten immediately. However, there was no significant difference in the distance, height, or time taken to cache for caches of different-sized mealworms. Secondly, I determined how robins responded when their cached mealworms were pilfered by a human observer. After birds made 10 caches, I stole the three nearest caches while in sight of the caching bird. If birds perceived me as a pilferer, this should lead to future caches being stored higher up and further away from the observer. As expected, I found that robins stored food further away and more often out of sight when caching the next day in my presence. Lastly, I determined whether robins altered their caching behaviour in relation to the attentional gaze of an observer. To reduce the risk of pilfering, robins should alter their caching behaviour if being observed directly. I tested this hypothesis by altering my direction of gaze while birds cached. However, no differences were found in time taken to cache, caching distance or caching height in relation to my attentional gaze. Overall, my results indicate that caching food is dependent on food size and previous experience of cache pilferage but that more subtle cues, such as direction of gaze, are not used when robins decide on cache location. This work highlights the key roles of both prey size and risk of pilferage in the decision making process of whether or not a robin decided to cache a particular prey item, and if a cache is made, the location of these caches.

CHAPTER 1

Introduction

1.1 General introduction

When many animals find food they do not eat it immediately, nor do they ignore it or give it to a conspecific. Instead they shift and store the food for latter consumption (Andersson & Krebs 1978; Smith & Reichman 1984). This behaviour is known as caching or food hoarding/storing (for a review, see Vander Wall, 1990). Many birds and mammals are well known to cache food (Roberts 1979; Smith & Reichman 1984). Humans are also prolific cachers and we tend to put all our personal food into one or a few locations, namely the kitchen. However, relatively few invertebrates have been reported to cache food, except for some orb web spiders (Eberhard 1967), the crab *Pilumnus vespertilio* (Kyomo 1999) and hymenopterans such as the honey bee *Apis mellifera* (Champion de Crespigny *et al.* 2001). One of the most well known groups of caching animals are squirrels in northern hemisphere forests. Every year there is a seasonal surplus of acorns (*Quercus* spp.) in autumn, and grey squirrels (*Sciurus carolinensis*) exploit the temporary abundance of food by harvesting far more acorns than they can consume immediately and instead they store them in many locations throughout their territory (Cahalane 1942). During winter and spring when acorns are no longer available from the trees, the squirrels retrieve the acorns they stored and use them to survive through this period of limited food supply. For squirrels and other animals, caching is more complex than simply storing food for later use, and instead requires decisions about when to cache, where to cache, how much to put in each cache, and whether to defend the cache. Empirical evidence from a variety of birds and mammals suggests that the likelihood of caching can be influenced by the perishability, handling time, and value of the food item, as well as the presence of potential cache robbers (Cristol 2001). This makes caching an economic decision and requires a certain level of cognitive development (Preston *et al.* 2005).

American kestrels (*Falco sparverius*) also cache prey, and like many caching animals, they tend to eat until they are satiated and then use the remaining daylight hours to forage and cache further surplus food that is then retrieved near the end of the day (Collopy 1977). By continuing to hunt immediately after capturing prey, kestrels increase the chance of obtaining food which might not be available later. If this extra food is stored, it can be retrieved later when prey may be scarce (Collopy 1977). Thus, caching can be a way of maximising foraging opportunities. Many wintering birds also cache food, and it was originally thought to be a strategy to externally accumulate energy reserves (as opposed to internally storing energy as fat) during the day to survive overnight fasting (Ketterson & Nolan Jr. 1978). However, there is now general agreement that caching is most likely an adaptation to cope with temporal food scarcity (De Kort *et al*. 2006; Roberts 1979). Therefore animals store food when it is plentiful and retrieve it at a time when food is scarce. In other words, caching provides a way to cope with unpredictable food supplies.

Animals distribute their caches in a number of ways; the extremes of this range are called larder hoarding (highly clumped) and scatter hoarding (highly dispersed). Squirrels and humans are examples at the two extreme ends on the caching spectrum, with humans storing most of their food in a single large larder, while squirrels disperse their food in a large number of caches but with each containing only a few items. Larder hoarding is a good strategy when an animal can defend or conceal a single cache from competitors (Smith & Reichman 1984). For example, Tengmalm's owl (*Aegolius funereus*) cache in their nest holes. Such caches are relatively safe from pilfering as the opening is too small for large birds of prey to enter and the owls are able to defend their caches from smaller birds (Korpimaki 1987). Some carnivores, such as leopards (*Panthera pardus*) and brown bears (*Ursus arctos*), prey on large animals that can also serve as a larder as the entire item

cannot be eaten in one feeding episode. In contrast, scatter hoarding is a good strategy for animals that cannot reliably defend a single cache. These animals benefit by "not putting all their eggs into one basket". Instead, they make many caches with one or a few pieces of food in each. Despite birds and mammals independently evolving caching behaviours, patterns of scatter hoarding are remarkably similar between these two groups, both in terms of behaviour and in correlations with how the brain is structured (Sherry *et al.* 1992; Sherry & Duff 1996).

The number of caches that different scatter-hoarding species create varies greatly. Pravosudov (1985) studied scatter hoarding in the Siberian tit (*Poecile cinctus*) and recorded over 500,000 caches by one individual over a year. By scattering caches, individuals increase dispersion and reduce the net energy gain for a pilferer to search and steal from a cache so that it becomes more profitable to forage for its own food (Smith & Reichman 1984). The propensity of some species to create scatter hoards led Stapanian & Smith (1984) proposed the 'optimal cache spacing theory' (henceforth, OCST); the theory predicts that scatter-hoarding animals should distribute their caches in a way that reduces the risk of pilfering. Pilferers who do not know the location of another's cache, yet incidentally discover one may search for additional caches nearby, so the greater the distribution of caches, the less likely a naive individual is to find a second cache before it abandons the search (Stapanian & Smith 1978). The theory also suggests that caching food at lower densities requires more travel time and effort. Caching animals should 'optimally' balance the benefit of retrieving more of its own caches and the costs of distributing food to more distant cache sites. Therefore, individual caches should be sequentially placed farther from the food source in order to maintain optimal cache densities.

The duration of a cache can also vary from species to species. Many birds, such as willow tits (*Parus montanus*) (Brodin & Kunz 1997), northwestern crows (*Corvus caurinus*) (Vander Wall 2003) and South Island robins (*Petroica a. australis*) retrieve stored food within a few days of storage (Powlesland 1980). Suggested benefits of short term hoarding are to (1) even out fluctuations in the food supply (Vander Wall 1990), (2) secure as much of a temporary surplus of food as possible from competitors (Lucas & Walter 1991), (3) secure access to food when it is optimal, for example, for lean birds in bad weather and therefore, as insurance against future shortage (McNamara & Houston 1986), or (4) minimise the time that body fat has to be carried around as an energy reserve for night time fasting (thereby an individual can stay lean to avoid mass dependent costs) (McNamara *et al.* 1990). There is also intraspecific variation in caching behaviour; it may vary according to age (Maccarone 1987), sex (Burns 2009; van Horik & Burns 2007), season (Steer & Burns 2008) and social condition (Burns & Steer 2006).

Food availability can affect caching behaviour and it may vary for a number of reasons. Food can be unpredictable due to unsuitable weather, or its availability may be variable if it is related to diurnal, tidal or annual cycles. As a result, it may be advantageous for food to be cached for many months or only a matter of hours, depending on species and environmental conditions.. In the seasonal environments typically found at higher latitudes, reproduction generally takes place when food is abundant. For example, most temperate passerines breed during summer when prey abundance is high, and caching seldomly occurs at this time (Pravosudov & Lucas 2001). However, as prey abundances decline in the non-breeding season, some birds may store food to offset periods of food scarcity (Pravosudov & Lucas 2001). There are many variables that affect the amount of food available at any given time; the amount of food produced, competition within and

between species, or the cost of foraging in terms of, for example, predation risk. In particular, winter is a time of limited food availability for many animals in temperate and high latitude environments, as shorter days, longer nights, cooler temperatures, more extreme weather, and reduced food availability make it increasingly difficult to meet greater thermoregulatory demands (Nolan Jr. & Ketterson 1983). Individuals in the more northern populations of a given species tend to be heavier because body fat provides insulation and protection from below freezing winter nights (great tit, *Parus major*, Hafthorn 1972; Gambel's white-crowned sparrows, *Zonotrichia leucophrys gambelii*, King & Mewaldt 1981; dark-eyed juncos, *Junco hyemalis*, Nolan Jr. & Ketterson 1983), and this seasonal change can in turn affect whether food is stored as a cache or stored as body fat.

Several researchers, working mainly with small passerines, have suggested that small birds store only enough fat to ensure overnight survival, and that the observed trends in body mass reflect the fact that birds may simply store more fat to survive the colder and/or longer nights experienced during midwinter or at higher latitudes (Blem 1976; Blem & Pagels 1984). The assumption that small birds live from day to day (e.g. Newton 1972), being able to survive only about one night without food, is common, but not supported (Ketterson & Nolan Jr. 1978). A more plausible temperature-related hypothesis was forwarded by Evans (1969), who suggested that (small) birds maintain enough fat reserves to survive the coldest night they might expect at a given location, hence the geographical and temporal trends in body mass (Lima 1969). In other words, if animals do not consume a sufficient amount of food and energy to remain healthy, this can quickly lead to death on a cold night in a cold climate. For example, Eurasian red squirrels (*Sciurus vulgaris*) that retrieve the most nuts have the greatest body mass and highest winter survival rate (Wauters & Lens 1995). It is not surprising then that caching animals

are more common at higher latitudes where the seasons are more pronounced than at lower latitudes. For these reasons it can be advantageous to cache food when it is available as insurance against stochastic fluctuations in environmental conditions, and where storing and retrieving caches minimises the stochasticity of food availability.

McNamara *et al.* (1990) designed the dynamic optimisation model (DOM) to theoretically test when a bird should be more likely to cache as a result of the availability of food and their own energy levels. DOM is an uncomplicated cost and benefit analysis. They found that it is profitable for a caching animal to do the following as part of its 'optimal daily routine': (1) cache early in the day and retrieve in the later part of the day; (2) cache when food is more unpredictable or variable; (3) cache less when the rate of consumption increases; and (4) increase the frequency of caching when the costs of eating and carrying the fat reserves are high and when overnight energy expenditure is high (McNamara *et al.* 1990).

Although trade-offs between internal and external storage are predicted by DOM (McNamara *et al.* 1990), empirical support is mixed (Burns 2009). In a theoretical model by Brodin (2000), mortality was twice as high for non-hoarders as for hoarders during the worst possible conditions. Furthermore, theoretical models suggest that because caching is a means of externally storing energy, animals can maintain lower body mass and avoid the costs of internally storing food as fat, such as outrunning and outmanoeuvring predators (Waite & Grubb Jr. 1988). Thinner birds might also have a smaller risk of predation as animals require more time foraging if metabolism is mass dependent and thus more time can be spent in safe microhabitats and/or being vigilant for predators (Brodin 2010; Houston & McNamara 1993; Pravosudov & Lucas 2001). Many studies have confirmed that the evening mass of small birds drops by between 5 and 10 % after a winter's night

(Ketterson & Nolan Jr. 1978; Lehikoinen 1987). Equivalent data is limited for small birds from the Southern Hemisphere. Chan (1994) found that silvereyes (*Zosterops lateralis*) from Tasmania had an average daily fluctuation of their mass of 8.3%. Land areas are typically smaller in the Southern Hemisphere; therefore winter weather is relatively less intense (Chan 1994). However, there are also costs associated with storing food as caches, such as; food spoiling, pilfering by competitors and that their locations may be forgotten over time (Vander Wall 1990). These costs highlight the problem of theoretical models: they are often (at least early models) simplistic compared to the natural world and its multitude of variables.

Before caching any food, animals should make decisions about the type and amount of food to cache, the cache location, when to cache it, and the duration of the cache. These decisions may be directed by the animal's anatomy, physiology, and/or motivational state, as well as by ecological factors within the environment they inhabit. To make these decisions, animals also have to process complex information, and cognitive abilities may constrain complex decision making processes (De Kort & Clayton 2006). One strategy to recover caches is to remember the exact location of each cache. This is termed the cache recovery phase, and memory is particularly important for caching animals because if they fail to retrieve their caches then they risk starvation (Vander Wall, 1990). Several studies have examined specialisations in brain structures with known learning and memory functions (Hampton *et al.* 1995). In an early study, Krushinskaya (1966) created surgical lesions on various areas of the brain to show that Eurasian nutcrackers (*Nucifraga columbiana*) use spatial memory to relocate caches. Both Eurasian nutcrackers and others species have been found to be dependent on an intact hippocampus for finding their caches (Sherry 1989). In a more recent study, hippocampal aspiration

lesions in black-capped chickadees (*Poecile atricapillus*) impaired retrieval but they continued to cache and search as intensely as control birds (Sherry & Vaccarino 1989). The number of items cached and the length of time they are left before recovery varies from species to species, and these differences are reflected in brain structure (Lucas *et al.* 2004). For example, Pravosudov & Clayton (2002) found that black-capped chickadees from lower latitudes had larger hippocampi than individuals from higher latitudes. The hippocampus is also larger in caching birds than in non-caching birds (Krebs *et al.* 1989). Food storing in birds has thus become an important model system for the study of memory and cognition, with most studies using members of the Corvidae (crows, jays, nutcrackers, magpies, etc.) and Paridae (titmice and chickadees), but there are also some studies in other taxa, for example, some woodpeckers (Brodin & Bolhuis 2008; Volman *et al.* 1997). Even more importantly, there is also now good evidence from anatomy, lesions and electrophysiology experiments, that in all the vertebrate groups the hippocampus is important for spatial memory (Colombo & Broadbent 2000).

Food-caching is a behaviour that is orientated toward future needs. Indeed, the act of hiding food is without immediate benefit and yields its return only when the bird comes to recover the caches it made. Given that caching birds are dependent on finding a significant number of these caches for survival, it seems likely that the selection pressure for memory would have been particularly strong (Griffiths *et al.* 1999). At issue, however is whether such behaviour can be explained by simpler mechanisms, such as knowing rather than remembering where they hid their food caches (Clayton *et al.* 2009). Episodic and sematic memory are thought to be two separate states of awareness; episodic memory requires an awareness of reliving a past event and of mentally travelling back to relive the event, whereas semantic memory only involves an awareness of the acquired information

without any need to travel mentally back in time to personally re-enact the past event (Gardiner 2001). The question of whether animals can mentally travel in time remains controversial (e.g. to remember where it made a cache by mentally re-enacting the creation of the cache), but has at least challenged the idea that non-human animals cannot understand forethought and episodic memory.

There are also costs involved in altering cache spacing and cache number. Memory demands are higher when an animal must retrieve a larger number of caches, and this cost is reflected in the relative increase in hippocampus size seen in animals that scatter-hoard compared with animals that larder-hoard (Jacobs 1992; Sherry *et al.* 1992). Predation risk also increases as a function of exposure during travel time, so there is a greater risk of detection by predators associated with greater cache dispersion (Daly *et al.* 1990). Animals that rely on caching food should have evolved to respond adaptively to the changing costs and benefits associated with it by modulating their caching decisions in accordance with such factors as the value of the food to be cached, the predation risk associated with caching and recovery, and the risk of cache pilferage (Leaver 2004). Foraging theory predicts that animals will conduct a more intensive search (investing more effort in searching over the same area) in the surrounding area after encountering an item of food when foraging (Benhamou 1992), and obviously this also applies to animals that find an unfamiliar food cache when foraging. Furthermore, theoretical models of cache spacing predict that a "pilferer" will conduct a more intensive search for additional caches after encountering a cache containing a highly valuable food than if it encountered a less valuable food (Stapanian & Smith 1978; Stapanian & Smith 1984). As a result, animals must compensate by caching more valuable foods at lower densities (Stapanian & Smith 1978; Stapanian & Smith 1984). Food 'value" is measured in various ways; for example,

depending on the species in question, value can be measured in caloric value, nutritional content, or time taken to perish.

1.2 Outline of thesis

The aim of my thesis was to examine the effects of food size (Chapter 2), pilfering (Chapter 3) and attentional gaze (Chapter 4) on the caching behaviour of the South Island robin. As with other caching species, I assumed that the caching behaviour of robins was the product of natural selection and will have evolved in ways that are adaptive. Thus, I expected robins to alter their propensity and pattern of caching in response to changes in food value and the risk of pilferage. By systematically altering prey size and the risk of pilferage, I experimentally tested whether robins change their caching behaviour in ways that maximise the value of their caches and protect their caches from pilferers. The results of my experiments are presented in the next 3 chapters (Chapters 2-4), and then I conclude with a general discussion (Chapter 5).

In Chapter 2, I tested the role of size of food items on the caching behaviour of South Island robins. Larger food items are more rich in energy and I fed mealworms in one of five weight categories to robins to see if prey size affected caching behaviour. I predicted that as larger mealworms are more valuable, robins should cache in ways to protect these larger caches. I also predicted that larger items will more regularly be cached, whilst smaller items will be regularly eaten because their energy value is too low to be worth caching.

In Chapter 3, experimental pilfering of caches was used to test if increased risk of theft changes the subsequent caching behaviour of robins. Caching animals are expected to

have evolved strategies to protect their food from pilferers. Pilfering could be detrimental to the survival of the caching animal because time and energy is wasted. If robins directly see me pilfering their caches, I predicted they should recognise me as a threat and alter their future caching behaviour (e.g. cache further away and higher up in trees) to protect their caches.

In Chapter 4, I tested the effect of a human observer's attentional gaze of the caching behaviour of robins. I presented mealworms to robins in ways that I predicted to represent different levels of threat of pilferage. When feeding robins mealworms, I tested whether the caching locations of robins differed when I looked directly at them compared to when I looked either to the left or right or in the opposite direction of the robin. In a second experiment, I also tested if robins would cache differently when I stood varying distances away from the feeding circle. I predicted that the direction of my gaze at the robin and my distance to them when feeding should reflect differing levels of threat of pilfereage to the robin and as a result they should cache further away and higher up in trees.

Finally, in Chapter 5, I review the results of my experiments and put them into a broader context of caching. I also suggest future avenues of research, and highlight the value of the South Island robin as a model species for studying the caching behaviour of birds.

1.2 Literature cited

Andersson, M. & Krebs, J. 1978. On the evolution of hoarding behaviour. *Animal Behaviour*, **26**, 707-711.

Benhamou, S. 1992. Efficiency of area-concentrated searching behaviour in a continuous patchy environment. *Journal of Theoretical Biology*, **159**, 67-81.

Blem, C. R. 1976. Patterns of lipid storage and utilization in birds. *American Zoologist*, **16**, 671-684.

Blem, C, R., Pagels & J, F. 1984. Mid-winter lipid reserves of the golden-crowned kinglet. *The Condor*, **86**, 491-492.

Brodin, A. 2000. Why do hoarding birds gain fat in winter in the wrong way? Suggestions from a dynamic model. *Behavioral Ecology*, **11**, 27-39.

Brodin, A. 2010. The history of scatter hoarding studies. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **365**, 869-881.

Brodin, A. & Kunz, C. 1997. An experimental study of cache recovery by hoarding willow tits after different retention intervals. *Behaviour*, **134**, 881-890.

Brodin, A. & Bolhuis, J. J. 2008. Memory and brain in food-storing birds: space oddities or adaptive specializations? *Ethology*, **114**, 633-645.

Burns, K. 2009. Fine-scale food hoarding decisions in New Zealand robins (*Petroica australis*): is inter-sexual competition important? *Journal of Ornithology*, **150**, 321-328.

Burns, K. C. & Steer, J. 2006. Dominance rank influences food hoarding in New Zealand Robins *Petroica australis*. *Ibis*, **148**, 266-272.

Cahalane, V. H. 1942. Caching and recovery of food by the western fox squirrel. *The Journal of Wildlife Management*, **6**, 338-352.

Champion de Crespigny, F. E., Herberstein, M. E. & Elgar, M. A. 2001. Food caching in orb-web spiders (Araneae: Araneoidea). *Naturwissenschaften*, **88**, 42-45.

Chan, K. 1994. Winter body mass and overnight energetics of a south temperate passerine. *The Auk*, **111**, 721-723.

Clayton, N. S., Russell, J. & Dickinson, A. 2009. Are animals stuck in time or are they chronesthetic creatures? *Topics in Cognitive Science*, **1**, 59-71.

Collopy, M. W. 1977. Food caching by female American kestrels in winter. *The Condor*, **79**, 63-68.

Colombo, M. & Broadbent, N. 2000. Is the avian hippocampus a functional homologue of the mammalian hippocampus? *Neuroscience & Biobehavioral Reviews*, **24**, 465-484.

Cristol, D. A. 2001. American crows cache less preferred walnuts. *Animal Behaviour*, **62**, 331-336.

Daly, M., Wilson, M., Behrends, P. R. & Jacobs, L. F. 1990. Characteristics of kangaroo rats, *Dipodomys merriami*, associated with differential predation risk. *Animal Behaviour*, **40**, 380-389.

De Kort, S. R. & Clayton, N. S. 2006. An evolutionary perspective on caching by corvids. *Proceedings: Biological Sciences*, **273**, 417-423.

Eberhard, W. G. 1982. Behavioral characters for the higher classification of orb-weaving spiders. *Evolution*, **36**, 1067-1095.

Evans, P. R. 1969. Winter fat deposition and overnight survival of yellow buntings (*Emberiza citrinella L.*). *Journal of Animal Ecology*, **38**, 415-423.

Gardiner, J. M. 2001. Episodic memory and autonoetic consciousness: a first–person approach. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, **356**, 1351-1361.

Griffiths, D., Dickinson, A. & Clayton, N. 1999. Episodic memory: what can animals remember about their past? *Trends in Cognitive Sciences*, **3**, 74-80.

Haftorn, S. 1972. Hypothermia of tits in the arctic winter. *Ornis Scandinavica*, **3**, 153-166.

Hampton, R. R., Sherry, D. F., Shettleworth, S. J., Khurgel, M. & Ivy, G. 1995. Hippocampal volume and food-storing behavior are related in parids. *Brain, Behavior and Evolution*, **45**, 54-61.

Houston, A. I. & McNamara, J. M. 1993. A theoretical investigation of the fat reserves and mortality levels of small Birds in winter. *Ornis Scandinavica*, **24**, 205-219.

Jacobs, L. F. 1992. Memory for cache locations in Merriam's kangaroo rats. *Animal Behaviour*, **43**, 585-593.

Ketterson, E. D. & Nolan, V., Jr. 1978. Overnight weight loss in dark-eyed juncos (*Junco hyemalis*). *The Auk*, **95**, 755-758.

Ketterson, E. D. & Nolan Jr., V. 1982. The role of migration and winter mortality in the life history of a temperate-zone migrant, the dark-eyed junco, as determined from demographic analyses of winter populations. *The Auk*, **99**, 243-259.

King, J. R. & Mewaldt, L. R. 1981. Variation of body weight in Gambel's white-crowned sparrows in winter and spring: latitudinal and photoperiodic correlates. *The Auk*, **98**, 752-764.

Korpimaki, E. 1987. Prey caching of breeding Tengmalm's Owls *Aegolius funereus* as a buffer against temporary food shortage. *Ibis*, **129**, 499-510.

Krebs, J. R., Sherry, D. F., Healy, S. D., Perry, V. H. & Vaccarino, A. L. 1989. Hippocampal specialization of food-storing birds. *Proceedings of the National Academy of Sciences*, **86**, 1388-1392.

Krushinshaya, N. L. 1966. Some complex forms of feeding behaviour of the nutcracker after removal of the archeocortex. *Zhurn Evol Biokhim Fizio*, **2**, 563-568. Cited in **Sherry, D. F. & Vaccarino, A. L.** 1989. Hippocampus and memory for food caches in black-capped chickadees. *Behavioral Neuroscience*, **103**, 308-318.

Kyomo, J. 1999. Feeding patterns, habits and food storage in *Pilumnus vespertilio* (Brachyura: Xanthidae). *Bulletin of Marine Science*, **65**, 381-389.

Leaver, L. A. 2004. Effects of food value, predation risk, and pilferage on the caching decisions of *Dipodomys merriami*. *Behavioral Ecology*, **15**, 729-734.

Lehikoinen, E. 1987. Seasonality of the daily weight cycle in wintering passerines and its consequences. *Ornis Scandinavica*, **18**, 216-226.

Lima, S. L. 1986. Predation risk and unpredictable feeding conditions: determinants of body mass in birds. *Ecology*, **67**, 377-385.

Lucas, J. R. & Walter, L. R. 1991. When should chickadees hoard food? Theory and experimental results. *Animal Behaviour*, **41**, 579-601.

Lucas, J. R., Brodin, A., de Kort, S. R. & Clayton, N. S. 2004. Does hippocampal size correlate with the degree of caching specialization? *Proceedings of the Royal Society of London. Series B: Biological Sciences*, **271**, 2423-2429.

Maccarone, A. D. 1987. Age-class differences in the use of food sources by European starlings. *The Wilson Bulletin*, **99**, 699-704.

McNamara, J. M. & Houston, A. I. 1986. The common currency for behavioral decisions. *The American Naturalist*, **127**, 358-378.

McNamara, J. M., Houston, A. I. & Krebs, J. R. 1990. Why hoard? The economics of food storing in tits, Parus spp. *Behavioral Ecology*, **1**, 12-23.

Newton, I. 1972. Finches. Collins, London.

Nolan Jr, V. & Ketterson, E. D. 1983. An analysis of body mass, wing length, and visible fat deposits of dark-eyed juncos wintering at different latitudes. *The Wilson Bulletin*, **95**, 603-620.

Powlesland, R. G. 1980. Food storing behaviour of the South Island robin. *Mauri Ora*, **8**, 11-20.

Pravosudov, V. V. & Clayton, N. S. 2001. Effects of demanding foraging conditions on cache retrieval accuracy in food-caching mountain chickadees (*Poecile gambeli*). *Proceedings of the Royal Society of London. Series B: Biological Sciences*, **268**, 363-368.

Pravosudov, V. V. & Lucas, J. R. 2001. A dynamic model of short-term energy management in small food-caching and non-caching birds. *Behavioral Ecology*, **12**, 207-218.

Preston, S. D. & Jacobs, L. F. 2005. Cache decision making: the effects of competition on cache decisions in merriam's kangaroo rat (*Dipodomys merriami*). *Journal of Comparative Psychology*, **119**, 187-196.

Roberts, R. C. 1979. The evolution of avian food-storing behavior. *The American Naturalist*, **114**, 418-438.

Sherry, D. F. 1989. Food Storing in the Paridae. *The Wilson Bulletin*, **101**, 289-304.

Sherry, D, F., Duff & S, J. 1996. Behavioural and neural bases of orientation in food-storing birds. *Journal of Experimental Biology*, **199**, 165-172.

Sherry, D. F., Jacobs, L. F. & Gaulin, S. J. C. 1992. Spatial memory and adaptive specialization of the hippocampus. *Trends in Neurosciences*, **15**, 298-303.

Smith, C. C. & Reichman, O. J. 1984. The evolution of food caching by birds and mammals. *Annual Review of Ecology and Systematics*, **15**, 329-351.

Stapanian, M. A. & Smith, C. C. 1978. A model for seed scatterhoarding: coevolution of fox squirrels and black walnuts. *Ecology*, **59**, 884-896.

Stapanian, M. A. & Smith, C. C. 1984. Density-dependent survival of scatterhoarded nuts: an experimental approach. *Ecology*, **65**, 1387-1396.

Steer, J. & Burns, K. C. 2008. Seasonal variation in male-female competition, cooperation and selfish hoarding in a monogamous songbird. *Behavioral Ecology and Sociobiology*, **62**, 1175-1183.

Vander Wall, S. B. 1990. Food hoarding in animals. The University of Chicago Press, Chicago.

Vander Wall, S. B. & Jenkins, S. H. 2003. Reciprocal pilferage and the evolution of food-hoarding behavior. *Behavioral Ecology*, **14**, 656-667.

van Horik, J. & Burns, K. C. 2007. Cache spacing patterns and reciprocal cache theft in New Zealand robins. *Animal Behaviour*, **73**, 1043-1049.

Volman, S. F., Grubb, J. T. C. & Schuett, K. C. 1997. Relative hippocampal volume in relation to food-storing behavior in four species of woodpeckers. *Brain, Behavior and Evolution*, **49**, 110-120.

Waite, T. A. & Grubb Jr., T. C. 1988. Diurnal caching rhythm in captive white-breasted nuthatches *Sitta carolinensis*. *Ornis Scandinavica*, **19**, 68-70.

Wauters, L. A. & Lens, L. 1995. Effects of food availability and density on red squirrel (*Sciurus vulgaris*) reproduction. *Ecology*, **76**, 2460-2469.

CHAPTER 2

Prey size and caching behaviour in the South Island robin (*Petroica australis australis*)

2.1 Abstract. – Natural selection should favour animals that maximise their net rate of energy intake while foraging by being selective eaters. For predators, this means they should select larger and more valuable prey items, as long as such prey can be handled easily. Studies have shown that some scatter-hoarding animals preferentially cache larger food items and cache items at low density far from the food source. Caching at low densities should protect food from theft if pilferers search for food at random. The South Island robin (*Petroica australis australis*) is a short-term scatter-hoarder and readily accepts and caches mealworms (*Tenebrio molitor*) provided by a researcher. This provides an ideal opportunity to test if free-living robins cache experimentally provided food in a way that minimises pilfering. Cache spacing behaviour was studied by presenting male robins with 5 different size categories of mealworms. I found that robins were significantly more likely to cache large mealworms while small mealworms were eaten immediately. However, there were no significant difference in the distance, height, or time taken to cache for caches of different-sized mealworms. Robins may preferentially cache large food items, as this will provide them with more energy when faced with a lack of food. In contrast, caching smaller food items provides little energetic return, at least relative to that of the energetic cost of caching the item in the first place. I suggest the reason robins do not alter cache placement with prey size is because they perceive the risk of pilfering to be small as other robins are unlikely to find cached food unless they have witnessed the cache being made. I suggest robins did not alter cache placement with prey size because they perceived variation in the risk of pilfering with prey size to be small relative to the range of prey sizes that they actually cached.

2.2 Introduction

Optimal-foraging theory (OFT) states that for predators to be efficient they need to maximise their net rate of energy intake while foraging by selecting items based on their profitability (e.g., energy content per unit handling time; Emlen 1966; Charnov 1976). Predators that detect, capture and prepare prey must do so with enough efficiency that they do not expend more energy than they obtain. OFT predicts that in the course of achieving an optimal diet, natural selection will favour predators that: (1) preferentially exploit the more profitable prey types, (2) do not eat unprofitable prey no matter how common they are, and (3) are more selective when profitable prey are common (Charnov 1976; Pyke *et al* 1977). A number of studies have found empirical support for these predictions. For example, house martins (*Delichon urbica*), tree swallows (*Tachycineta bicolor*) and barn swallows (*Hirundo rustica*) discriminate between prey items primarily by size when they feed nestlings (Bryant & Turner 1982; Quinney & Ankney 1985). These species prefer larger, more valuable prey items and show an increase in the number of prey species they will exploit when there is a decrease in relative rate of encounter with larger items (Quinner & Ankney 1985).

Animals that cache or hoard food for later consumption are also predicted to store food in an optimal manner. It is predicted by optimal cache spacing theory (OCST) that high value food items should be cached at lower densities than food items of lesser value (Galvez *et al.* 2009). Several empirical studies on scatter-hoarding rodents and birds have found that size of prey is an important factor in OCST; for example, more nutritious seeds are cached further away from the initial location of the food item (and thus at lower densities) than small seeds (Jansen & Forget 2001; Vander Wall 2003; Jansen *et al.* 2004; Leaver 2004; Galvez *et al.* 2009). Jansen *et al.* (2004) argued that the value of food to

hoarders is determined not only by the nutritional content but also by the overall availability of food. Therefore, OCST also predicts that cache spacing and cache robbery are dependent on temporal and spatial variation in food availability.

Whether an animal decides to cache a particular food item or to eat it immediately can also depend on prey size. Moles *et al.* (2003) found a variety of post-dispersal seed predators in Australia (mostly rodents) ate large seeds less often *in situ*, and instead they were more often cached. Wang & Chen (2009) likewise found Old World rodents were more likely to cache larger seeds and large seeds were cached further away from the seed source. In this study, the rodents had a large surplus of food, they ate very few (less than 4%) seeds immediately and well over half the seeds were not eaten or cached (Wang & Chen 2009). Jansen *et al.* (2004) found that rodents also removed large seeds faster, were more likely to scatter-hoard large seeds, and large seeds were dispersed farther away than smaller ones, resulting in a higher probability of seedling establishment for larger seeds. Larger seeds generally contain more energy and it may be that caching animals preferentially eat smaller prey items as the return in energy from the retrieved cache of small prey items is relatively less compared to the costs of caching than for larger prey items.

Predator-prey relationships involve a host of interacting variables that must be considered to understand these relationships fully. However, prey size is one variable expected to play a key role in prey selection. Indeed, predators might use prey size as a "rule of thumb" to estimate relative prey profitability for optimising diet selection. Many studies have demonstrated that rodents preferentially select large seeds more than small seeds (Moles *et al.* 2003; Wang & Chen 2009). Barnard & Brown (1981) examined prey choice in the common shrew (*Sorex araneus*) and found that given the encounter rate is

sufficiently high, shrews preferred larger pieces of mealworm, and they were also less selective when a competitor was present during a test. Some microcarnivorous fish also prefer to eat large invertebrate prey (Werner & Hall 1974; Rincon & Lobón-Cerviá 1999), although Bence & Murdoch (1986) found prey selection in mosquitofish (*Gambusia affinis*) was not size dependent. This is usually explained by optimal diet theory: the benefit obtained from a prey item increases rapidly with prey size, usually with little or no increment in the cost involved; thus the largest prey size is usually also the most profitable (Bence & Murdoch 1986). However, detectability of prey also increases with prey size and can lead to a non-random mix of available prey.

In this study I empirically tested whether the pattern of caching by the South Island robin (*Petroica australis australis*), measured in terms of distance and height of cache from food source, and the time taken to cache, correlated with prey size in a manner consistent with OCST. There are several reasons to suspect that robin should preferentially cache larger prey items: (1) larger prey may have a greater volume to surface ratio and thus stay fresher and/or do not dry up and harden; (2) by choosing large prey, robins need to keep track of fewer caches to obtain the same energy reward; (3) handling time for larger prey could be less as transporting a larger prey may be easier than transporting several smaller prey; (4) the reduced handling time of larger prey may reduce the risk of predation; and (5) the likelihood of interactions with conspecifics and would-be pilferers is reduced. However, there is little experimental evidence to support the above predictions and there have been few previous studies examining whether prey size affects caching behaviour.

Using prey items of differing size, I experimentally tested whether South Island robins (hereafter, robins) would alter their caching behaviour depending upon the size of

the prey. Specifically, I tested the following predictions: (1) robins will more often cache the largest prey and eat or ignore the smallest prey items; (2) robins will cache the largest prey further away from the food source; (3) robins will cache the largest prey higher up in the trees; and (4) robins will take more time to cache the largest prey.

2.3 Methods

Study site and species

I conducted the food caching experiments during the autumn (March-April) 2010 at two sites; Kowhai Bush and Waimangarara Forest, near the town of Kaikoura, on the east coast of the South Island of New Zealand. The two fragments of lowland bush contain a mix of broad-leaf and kanuka (*Leptospermum ericoides*) forest with an understorey of shrubs, vines and ferns. The Kaikoura area experiences a mild, temperate climate. A breeding population of approximately 28 South Island robin (hereafter, robin) were present at the time of the experiment. The breeding season of robins in this area starts in late July/August and most pairs have finished by the start of February (Powlesland, 1983). They may lay up to four clutches per season; robins tend to lay again if a whole clutch is lost, which often happens on the mainland because of predation. Male and female robins live in socially monogamous relationships and hold territories year round. Males are larger and can be aggressive and dominant over their mate (Alexander *et al.* 2005); however, both sexes forage together in the non-breeding season, suggesting that territory subdivision resulting from male aggression is uncommon (van Horik and Burns, 2007).

The South Island robin is a medium-sized (32-40 g), insectivorous passerine endemic to the South Island of New Zealand (Mackintosh & Briskie 2005). The South

Island robin is closely related to the Stewart Island robin (*P. a. rakiura*), and the North Island robin (*P. a. longipes*). All three subspecies are sometimes collectively referred to as New Zealand robin or bush robin, but Gill *et al.* (2010) recently split the New Zealand robin into two species, the North Island robin (*P. longipes*), and the South Island robin (*P. australis*), the latter which includes the Stewart Island subspecies. Each of the species/subspecies has slight variations in their plumage colouring, but they all have a near black body and white breast. The caching behaviour of *P. a. australis* is similar to that of *P. a. longipes* (Alexander *et al.* 2005). For this reason many references to robins throughout this thesis are in fact studies on the North Island robin.

The South Island robin was once found throughout the South Island, but the population has declined over the last few hundred years. The decline is predominantly the result of the introduction of mammalian predators and large-scale deforestation which peaked during two waves of human settlement, firstly by Polynesians and secondly by Europeans (Towns & Daugherty 1994; Worthy & Holdaway 2002). Robins have been translocated to several predator-free islands, where they can reach densities more than ten times higher than on the mainland. Mortality of clutches is high on these islands, quite possibly due to the low genetic variation coming from a very small founding population (as low as five on some islands) and inbreeding depression (Mackintosh & Briskie 2005). At present, robins are predominantly found where there are still large tracks of native forest although they are occasionally found in exotic plantations that are contiguous with native forest (Clout and Gaze 1994). Robins favour structurally simple (monospecific) forests with dense and even canopies, and extensive areas of ground covered leaf litter (Clout and Gaze 1994). Borkin *et al.* (2007) found the highest densities of robins in

manuka (*Leptospermum scoparium*)/kanuka forest and Douglas fir (*Pseudotsuga menziesii)* forest with sparse understorey.

Robins spend ~90% of their foraging time on and within 2 m of the forest floor; they search for prey in low lying vegetation, in and around logs, and in the soil litter (Powlesland 1981). They feed predominantly on earthworms, but will also eat slugs, insects, spiders and berries (Powlesland 1980). Hunting behaviours include hawking, flycatching, and gleaning. Robins will often use wing- and tail-flicking and foot trembling while searching for prey (Powlesland 1981). These behaviours appear to function in disturbing the leaf litter and soil, thus exposing prey or initiating prey to move, which the robins are able to locate by sound or movement.

Robins are well known to cache invertebrates when they have a temporary abundance of food. They have been seen to cache large invertebrates like earthworms and cicadas, but sometimes larger prey like weta are first broken up before the pieces are cached or eaten (Powlesland 1980). Smaller food items appear to be eaten immediately (Powlesland 1980) although this has not been quantified. They do most of their caching from April to July (autumn and winter), and the rate of caching drops over the breeding season while the parents are feeding their offspring (Steer & Burns 2008). Typically, robins cache and retrieve food on the same day (Powlesland 1980). Caching may occur at any time of the day, but mostly in the morning and retrieval tends to occur mostly around mid-afternoon (Powlesland 1980). It is probable that robins cache for only a day because, unlike seeds which are so commonly hoarded by many Northern Hemisphere species and stay fresh for many months after hoarding, invertebrates will rapidly go rotten once they are killed and then stored in moist, warm conditions prevailing in the area robins inhabit (Powlesland 1980). Most cached items are first punctured, which not only immobilises the

prey but may help to stick the prey to the cache site by the leaking body fluids (personal observation). Food is always cached close to where it was found, most often less than 10 m via flight to a tree (personal observation).

Like many species endemic to isolated islands, robins lack many antipredator behaviours towards mammals (Maloney & McLean 1995). Consequently, they appear fearless to researchers and can be fed by hand. They will readily participate in food-hoarding experiments where detailed behavioural observations can be made at close range and the exact quantity and quality of prey controlled systematically. In feeding experiments using mealworms (*Tenebrio molitor*) as prey, males aggressively defend food sources in all seasons (Burns & Steer 2006). Although females are subordinate, they display behavioural strategies to gain access to prey. First, females can rapidly grab prey when males leave it unattended. Second, during the breeding season females are often fed by their mate via nuptial feeding. Third, females often pilfer caches made by their mate. Sometimes food was pilfered and re-cached by either sex (Steer 2006). Steer & Burns (2008) suggest that such sex-specific strategies may play an important role in monogamous territorial birds by allowing both sexes to forage side-by-side. Interspecific pilferage by may also be important; birds (Steer 2006) and insects (Barr *et al.* 1996) also have a similar diet and may come across robins caches.

Field experiment

To determine if caching behaviour varies with prey size, I offered different-sized mealworms to robins and measured their caching patterns. Robins readily approach humans in a natural setting and cache mealworms hand fed to them within their territories.

I conducted a single feeding trial on each male robin (n = 13 birds). All birds were identified by permanent leg bands and sexes were confirmed with banding records. In the summer of 2009/2010 almost all the robins were banded at both field sites. Trials were conducted between 9 am and 4 pm (NZST) and were halted if interrupted by strong winds or moderate to heavy rainfall. Juveniles, whose sex is difficult to identify, were excluded from trials.

Robins were first located by sight or by their song. To attract robins to within a few metres, I used either clapping, singing, and pishing sounds, or by hitting broken branches against trees. In all cases, these noises attracted robins to my immediate vicinity. I also cleared a circular area of ground about 75 cm diameter of all dead leaves and ferns to use as the feeding point. I stood approximately 2 m from the feeding point during trials. Robins were readily attracted to the disturbed ground, perhaps to feed on the invertebrates uncovered. The experiments were only started when the males were accompanied by their partner in the nearby vicinity. When the male robin was within 4 m, I began the trial by throwing a mealworm into the centre of the feeding point. Mealworms were divided into one of 5 categories, depending upon their mass. Prior to the experiments, I weighed each mealworm (to 0.001 g) on an Ohaus Scout Pro Portable scale. The five categories were 0.030-0.060 g, 0.060-0.090 g, 0.090-0.120 g, 0.120-0.150 g and 0.150-0.180 g. I assumed that the mass of the mealworm was proportional to its energy value, with larger mealworms providing a robin with a larger source of energy than a smaller mealworm. Mealworms were thrown to the robins one at a time, and the size of the mealworm was randomly selected each time. The next mealworm was fed to the robin once the previous one had been eaten or the robin had returned after caching.

I conducted trials on only male robins, however, males were always accompanied by their mate at the start of trials. Only males were tested because females are subordinate and cache few mealworms because they are chased away by males (Burns 2009). Sometimes a rival (or neighbouring) male showed up at the trial; this interaction would usually result in one male chasing the other off. If the male did not return after 5 minutes then the trial was started again the following day. Most birds consumed 5 to 10 mealworms before starting to cache additional mealworms in nearby trees. I continued to feed mealworms to robins until they had cached 10. I decided to limit the number of caches to 10 mealworms because at some point usually beyond 10 worms the robins leave the feeding to point to do other behaviours such as territory defence or preening. A mealworm was defined as cached if it was transported in a robin's bill and deposited in a new location. All mealworms offered to birds were either consumed or cached, except on one occasion when a robin dropped the mealworm and it was lost in the undergrowth. Male robins consistently acquired the mealworms I threw out during trials; females either stood by but did not attempt to eat mealworms or they were chased away by their partner. However, females did acquire mealworms from their partner's caches often by pilfering (personal observation). Cached mealworms were first immobilised by being crushed between the bird's mandibles or pecked.

Statistical analysis

I quantified three dependent variables to characterise the effort (time + energy) spent caching a mealworm. First, I recorded the time from when the robin picked the mealworm up in its bill to when it returned to within 4 m of the feeding point. This is referred to as cache time, which is the time required to cache a prey item. I then measured both the

height and the distance of caches from the food source. This was done after the trial was complete to avoid disturbing caches and thereby potentially changing the subsequent caching behaviour of the birds. To remember locations of caches during the trial, I noted the direction, approximate height and distance, tree species, and any defining characteristics of the cache in a notebook. In all cases, I was successful in relocating caches after the trial was complete. Both distance and height were measured with a measuring tape. Distance was measured as the distance between the experimental food source (i.e., the location on the forest floor where the mealworms were placed) and the point on the ground below the cache site. Height was measured as the distance between the cache site and the point directly below on the forest floor. Data was tested for normality using D'Agostino & Pearson omnibus normality tests. As all treatments were found to be non-normal, I used non-parametric tests in the analysis. However, all data sets contained missing data and therefore the non-parametric Kruskal-Wallis tests had to be used. Dunn's multiple comparison tests were used to compare the medians of one size class to another size.

2.4 Results

Size class had a significant effect on whether or not a mealworm was cached (Figure 2.1; $K = 47.20$, $p < 0.0001$). Using Dunn's multiple comparison tests, it was found that there were significant differences between size class 1 and classes 3, 4 and 5, as well as size class 2 and classes 4 and 5. For all other tests there was no significant difference between size classes. Robins cached very few mealworms in the 2 smallest size classes (size 1 = 1.4% and size 2 = 4.4%, respectively), but cached over half of the mealworms in the 2 largest size classes (size 4 = 60.9% and 5 = 75.6%, respectively). The intermediate-sized

mealworms (size 3 = 40.8%) were more likely to be cached than the smaller mealworms but not cached as often as the larger mealworms. Mealworms that were not cached were all consumed and they were generally eaten at the feeding point or within 6 m while the bird was perched on a nearby tree trunk or branch.

For mealworms that were cached, there were no significant differences between the size of the mealworm and the horizontal distance to cache (Figure 2.2; $K = 4.55$, $p = 0.34$), height of cache (Figure 2.3; $K = 5.27$, $p = 0.26$) or the time it took to cache (Figure 2.4; $K = 2.46$, $p = 0.65$). The average distance mealworms were cached was 6.2 m (sd = 3.1) and the average height was 2.5 m (sd = 1.3).

Robins always ate some mealworms at the feeding points before beginning to cache. On average, the first ten mealworms given during trials have an 86% chance of being eaten. To see if this period of consuming mealworms directly affected caching behaviour, I re-analysed my data after excluding the outcomes of the first 10 mealworms as most of these were eaten immediately. As previously, the relationship between the proportion of mealworms cached and size class was still highly significant ($K = 45.27$, $p < 0.0001$). There were significant differences between size class 1 and classes 3, 4 and 5, as well as size class 2 and classes 3, 4 and 5. Thus, apart from the difference between size classes 2 and 3, the initial period of consuming most prey offered, did not appear to effect the subsequent pattern of caching behaviour.

2.5 Discussion

The results of my study show that prey size is an important factor in determining whether or not robins engage in caching behaviour. This is an important finding as prey size has

been mostly ignored in studies on the caching behaviour of birds (Bossema 1979; Waite 1992). My feeding experiments clearly demonstrate that robins choose which mealworms to eat immediately and which to cache later based on their size. Robins cached the two largest size classes of mealworms proportionately more often than they cached the two smallest size classes of mealworms. This suggests that robins can distinguish prey (at least similar looking prey that appears to only differ in girth and length) depending on its size. They then use this knowledge to decide whether to cache or not to cache food items. However, despite size playing a key role in their propensity to cache, prey size had no significant influence on the distance a prey item was cached, the time it took to cache, nor the height at which it was cached.

The results suggest robins have an ability to distinguish among prey items of differing size, but which are otherwise similar in colour and shape (at least to a human observer). It is known from numeracy studies that a variety of species of fish, reptiles, birds and mammals can select the larger of two quantities (usually less than four) innately, hence it is suggested that these animals have a rudimentary ability to count (e.g., mosquito fish, *Gambusia affinis,* Agrillo *et al.* 2008; New Zealand robins, *P. australis longipes*, Hunt *et al.* 2008; salamanders, *Plethodon cinereus*, Uller *et al.* 2003). However, when the relative difference between the two sets is great (i.e., 1:2), animals are better at counting than when 2 sets have a smaller relative difference (i.e., 3:4). In other words, they get worse at judging, raising the possibility that animals may not be comparing 'numbers' but comparing volumes. Whether robins use the same mechanism in numeracy decisions is unknown. It would be interesting to determine whether robins preferentially prey on one item rather than two items, if the single item was bigger than the combined size of the two items, or if robins would go for numerically greater quantity. On the other hand, targeting

the largest item could be the best choice, for example, if there is a greater handling time for two items than for only one item. Clearly, it would be interesting to evaluate if robins use volume rather than number to make caching decisions. It is conceivable that volume might be a better discriminatory cue when the birds dismember prey into different-sized caches (e.g., leg versus abdomen).

My study agrees with other studies in the caching literature, the majority of which have found that animals tend to cache significantly larger prey and seeds more often than they cache small to average sized food items (e.g., yellow pine chipmunks, *Tamias amoenus,* Vander Wall 1995; various rodent species, Xiao *et al.* 2004, Xiao *et al.* 2005). This supports the hypothesis that prey size has a key influence on the behaviour of caching animals. Several non-mutually exclusive explanations have been proposed for this behaviour. The most commonly described explanation is that large size is generally positively correlated with the energy content of the prey (Vander Wall 1995; Vander Wall & Jenkins 2003). Jansen *et al.* (2002) found that even if large seeds that have been cached germinate, they retain their nutritional value for longer than small seeds of the same species. By caching larger food items with greater total nutritional value, animals can reduce the number of caches needed to obtain the same absolute value as present in caches of smaller prey items (Jansen *et al.* 2002). If larger mealworms have a higher nutritional value (an assumption that seems reasonable), then robins likewise might be able to reduce cache number (and thus the costs of remembering cache location and the number of sites to defend) by preferentially caching only the largest prey items.

Pilfering of caches is one of the costs of caching food. It has been suggested that caching animals can reduce pilferage by storing more valuable food farther away from where they found it (Leaver 2004). In this case, density-dependent survivorship of caches

is likely to be higher because it is probably harder for pilferers to randomly discover caches at low density than at high density. However, this hypothesis has been seldom supported (Jansen *et al.* 2002). I found that cache spacing of mealworms by robins did not change with size of mealworms. This suggests that all caches are at the same risk of pilferage. Detailed estimates of rates of cache pilfering are not currently available, but it would be worthwhile determining if pilferage varies with the characteristics of a cache (i.e., its density, height, distance, etc.). As robins appear to use prey motion and sound to locate their prey (Brindle 1999), it is unlikely that they would be able to find a large number of caches using a simple random searching pattern (or if they did, that the return would be low). Furthermore, robins typically forage on the ground and most caches were made well away from ground level. Instead, it seems more likely that the risk of pilferage is greatest if the cache is seen by the pilferer while being put in place. The subject of how caching varies with a potential observer present is the subject of the next chapter (see chapter 3).

Due to the presence of introduced predatory mammals, the density of robins at my two Kaikoura field sites, Kowhai Bush and Waimangarara Forest, is very low. In contrast, robin populations on predator-free offshore islands are found at exceptionally high densities, sometimes exceeding 10 times that found on adjacent areas of the mainland. It is plausible that before the introduction of exotic predators and habitat destruction, robins would have historically been found at far higher densities than they are currently found at my Kaikoura field sites. However, it is not understood if robins on the mainland may have since altered their cache-spacing behaviour in response to the lower density, and presumably, lower risk of pilfering from conspecifics. It would be interesting to repeat my

study on several offshore islands, to see what effect, if any, density has on the caching strategies of robins.

As noted above, small mealworms were seldom cached and instead eaten either on the spot or taken a short distance away and consumed. This difference may be due to differences in handling time for smaller food items in relation to the gain in energy obtained. Handling time probably varies with prey size, but even if smaller items take less time to handle on a per capita basis, the cumulative time is likely to be greater for many smaller mealworms than one large mealworm that provides the same amount of nutritional value. Handling not only wastes time that could be spent searching for more food, territory defence or a number of other tasks but also exposes birds to greater predation risk (Lima 1986). A study on crows (*Corvus brachyrhynchos hesperis*) found they were more likely to cache less nutritious nuts, which required less time and energy to crack open (Cristol 2001). Therefore, handling time appeared to be important in deciding whether to cache the item or not. However, preparing and caching nuts is a different scenario to robins caching soft and fleshy mealworms. Sherry & McDade (1981) studied prey handling and prey selection in wild white-fronted nunbirds (*Monasa morphoeus*), and they found that handling costs were next to nothing compared to the benefits and they could not explain why there appeared to be a maximum limit in prey size. Handling costs are described as the time and energy spent modifying food items before consuming instead of ingesting food items immediately after capture. The swallowing threshold model suggests that food which is too large to be swallowed whole will be modified, and it predicts that as prey size increases then the handling costs will also increase (Kaspari 1990). But it appears from my personal observations that not a single mealworm was too large for robins to swallow whole because I never observed robins dismembering mealworms. During time spent

taming robins to my presence and to capture them for banding, I often feed them multiple mealworms at a time and it would not be unusual for the robins to fit seven mealworms simultaneously in their beak. Nevertheless, robins would often drop mealworms when they tried to hold this many mealworms in their beak at once. In this situation, trying to cache multiple mealworms at once incurs increased handling costs. Although the exact costs are unknown, I suspect that robins expend little or negligible time and energy preparing mealworms for caching and that the energy expenditure is probably quite similar for all size classes of mealworms.

A potential explanation for South Island robins having the ability to discriminate different sized prey may be that the size of prey is an integral part of their cache retrieval strategy. Although the ability to discriminate between prey sizes has yet to be tested in relation to a robin's age, they may learn this behaviour while caching food, retrieving caches and pilfering other robins' caches. There are a few non-mutually exclusive explanations that suggest why this behaviour may have arisen apart from the greater nutritional content found in larger prey. Firstly, if robins know the size of prey items in cache sites, it may help them prioritise which order to retrieve caches. For example, if food is cached singularly then they may go for the largest item, but if there are multiple items in each cache then it may be beneficial to retrieve the cache containing the collection of food items with the largest total size. It would be interesting to know if robins prioritise cache sites based on the number of food items or the volume of food. Knowing the size of food items may also help robins prioritise raids on caches made by its mate or rival robins; this would rely on them having seen them collect the food in the first place. Secondly, robins only store invertebrate prey, such as worms, insects and spiders. It is well known that dead animals or parts of animals are highly perishable. This is quite a different situation

compared to the many birds and rodents found in the northern hemisphere that cache seeds and nuts for many months without needing to be concerned with decomposition. Animal prey will start decomposing once dead and after some time the robins may no longer consume them. Time to spoilage has been found to influence the caching behaviour of arctic fox (*Vulpes lagopus*). Arctic fox eat lemmings, goslings and eggs, the latter of which contains antimicrobial agents that help prevent spoilage. Careau *et al.* (2007) found that eggs were carried further away for caching and more time was spent doing so. They also cached a greater proportion of eggs than either of the other two food types. Therefore, knowing how many items are stored in each cache site could help prioritise cache retrieval to minimise the loss of cached food items that spoil rapidly.

My results suggest that when the robins are making caches, they do not prioritise different sized mealworms, in terms of caching further away or higher in trees. Therefore my results are not consistent with the rate-maximisation model (Waite & Reeve 1992), which predicts that scatter hoarding animals should travel further to cache larger food items. Waite (1992) found the size of food items affected the Gray Jay's (*Perisoreus canadensis*) behaviour of how far to travel to store food, however, only one family comprising of three birds were tested in this study. But very few studies have looked at what factors affect the distance travelled by birds to cache their food (Bossema 1979; Waite 1992). Against my predictions, robins did not go to 'more effort' to cache high value food items. No matter what the size the mealworm was, there was no change in the distance it was cached, height cached or time spent caching.

Based on these findings I conclude that robins are not expending more energy to store greater value (nutritionally rich) prey. I can offer a few explanations why robins did not behave as I predicted based on OCST: (1) if robins spent more time handling large

prey, then this would make larger prey less valuable and the smaller prey more valuable than assumed based solely on the energy content of mealworms; (2) re-caching is common and therefore the importance of the initial location of the mealworm is of little value; (3) females pilfering their mates caches is common and if males tolerate a level of pilfering as part of a gesture to the mother of their offspring, then there is little benefit going to greater lengths to hoard food; (4) very few size 1 and size 2 mealworms were cached, thus the sample size was too small in this experiment to make reliable comparisons between caching behaviours for small and large mealworms. There are many more studies that have looked at the distances travelled by scatter-hoarding rodents (Galvez *et al.* 2009; Stapanian & Smith 1984; Vander Wall 1995). My finding that robins do not scatter high value food items further contrasts with the studies on scatter-hoarding rodents, which cache larger seeds further from the seed source (Jansen *et al.* 2004; Wang & Chen 2009). Rodents are also known to remove large seeds faster (Jansen *et al.* 2004) and they even removed more relatively larger seeds that had a lower nutritional value (Wang & Chen 2009). However, the rodents did not prefer the largest seeds but instead preferentially dispersed intermediate-sized seeds, suggesting that simple body size of the seed predator can limit the attractiveness of large seeds (Wang & Chen 2009). There are also many food item size-distance relationships that have been shown in a number of studies on a wide variety of foragers but in non-caching behaviours (see Stephens & Krebs 1986).

Some studies report that small prey items are often ignored because animals will expend more energy trying to catch them than the prey is actually worth and time is also being wasted that could be better spent targeting more larger and more profitable prey. In my study, small mealworms were never ignored. I suggest the reason for this is that robins would have expended little energy retrieving the prey when I threw the mealworms right in

front of them and because mealworms are slow moving animals that are incapable of escaping from the robins. Therefore, the handling costs would be very small and it would be in the robins' best interest to eat the mealworm no matter how big or small. Robins feeding on prey in the wild will often eat small invertebrates that are similar in size to the smallest mealworms used (personal observation). It has also been suggested that the ability to detect prey also increases with prey size. I am confident that this would not be the case for the robins in my experiments, although this wasn't tested, robins appeared to target and eat small mealworms just as readily as large worms. Robins often cannot see their prey because they are hidden within the soil, therefore their ability to judge the size of prey sometimes may be limited. But, on the other hand they may instead use sound and touch to determine how big prey are before pecking in the ground.

Marti & Hogue (1979) found that screech owls (O*tus asio*) took smaller prey above its availability. Increased hunger coupled with low prey density reduced preferential selection of prey by size. Considering I found that robins ate almost all small mealworms rather than caching them, this behaviour is not necessarily what robins foraging in the wild would display. It is well known that robins eat and cache very large invertebrates, such as weta; these are so large that the robin will dismember into smaller pieces (Powlesland 1980). However, smaller invertebrates such as worms and grubs make up the bulk of the robin's diet. If this is the case and also because it is assumed that robins are required to make caches to survive tough winter nights, it would be a reasonable assumption that there would be a need to cache smaller invertebrates. Because I was immediately feeding another mealworm to the robin once he had returned to the feeding point after eating or caching, I was increasing the prey density and I may have been rapidly reducing his hunger level. In effect I may have been altering their choice of which prey to cache, such

that they may have been predominantly only caching large sized mealworms because I was providing them with an abundance of food, albeit temporary.

Conclusions

The results of my experiments show that robins were more likely to cache large mealworms while small mealworms were eaten immediately. Although size of food was used by robins in their decision to cache, they did not change the distance, height, or time taken to cache in respect to the size of mealworms. As larger mealworms contain more energy than small mealworms, robins may preferentially cache large mealworms, as this will provide them with more energy when faced with a lack of food or more energy at the end of the day before they need to fast over night. In contrast, small prey items do not provide as much benefit because they provide little energetic return, at least relative to that of the energetic cost of caching the item in the first place. I suggest the reason robins do not alter cache placement with prey size is because they either perceive the risk of pilfering to be small as other robins are unlikely to find cached food unless they have witnessed the cache being made, or because the initial selectivity displayed by robins in only caching larger prey items means that variation in cached prey size was small and thus variance in cache sites relative to prey size are likewise small.

2.6 Literature cited

Agrillo, C., Dadda, M., Serena, G. & Bisazza, A. 2008. Do fish count? Spontaneous discrimination of quantity in female mosquitofish. *Animal Cognition*, **11**, 495-503.

Alexander, L., Duthie, C., Fyfe, J., Haws, Z., Hunt, S., Montoya, I., Ochoa, C., Siva, A., Stringer, L., van Horik, J. & Burns, K. C. 2005. An experimental evaluation of food hoarding by North Island robins (*Petroica australis longipes*). *Nortornis*, **52**, 138-142.

Barnard, C. J. & Brown, C. A. J. 1981. Prey size selection and competition in the common shrew (*Sorex araneus*). *Behavioral Ecology and Sociobiology*, **8**, 239-243.

Barr, K., Moller, H., Christmas, E., Lyver, P. & Beggs, J. 1996. Impacts of introduced common wasps (*Vespula vulgaris*) on experimentally placed mealworms in a New Zealand beech forest. *Oecologia*, **105**, 266-270.

Bence, J. R. & Murdoch, W. W. 1986. Prey size selection by the mosquitofish: relation to optimal diet theory. *Ecology*, **67**, 324-336.

Borkin, K. M., Goodman, A. J., Mayhew, K. & Smith, E. 2007. South Island robin (*Petroica australis australis*) abundance and leaf-litter invertebrates in plantation and native forest. *Notornis*, **54**, 65-70.

Bossema, I. 1979. Jays and Oaks: An Eco-Ethological Study of a Symbiosis. *Behaviour*, **70**, 1-117.

Brindle, C. 1999. Prey detection by South Island robins. B.Sc. Honours thesis, University of Canterbury, Christchurch, New Zealand.

Bryant, D. M. & Turner, A. K. 1982. Central place foraging by swallows (Hirundinidae): The question of load size. *Animal Behaviour*, **30**, 845-856.

Burns, K. C. & Steer, J. 2006. Dominance rank influences food hoarding in New Zealand Robins *Petroica australis*. *Ibis*, **148**, 266-272.

Burns, K. 2009. Fine-scale food hoarding decisions in New Zealand Robins (*Petroica australis*): is inter-sexual competition important? *Journal of Ornithology*, **150**, 321-328.

Careau, V., Giroux, J.-F. & Berteaux, D. 2007. Cache and carry: hoarding behavior of arctic fox. *Behavioral Ecology and Sociobiology*, **62**, 87-96.

Charnov, E. L. 1976. Optimal foraging, the marginal value theorem. *Theoretical Population Biology*, **9**, 129-136.

Clout, M. N. & Gaze, P. D. 1994. Effects of plantation forestry on birds in New Zealand. *Journal of Applied Ecology*. **21**, 795-815.

Cristol, D. A. 2001. American crows cache less preferred walnuts. *Animal Behaviour*, **62**, 331-336.

Emlen, J. M. 1966. The role of time and energy in food preference. *The American Naturalist*, **100**, 611-617.

Gálvez, D., Kranstauber, B., Kays, R. W. & Jansen, P. A. 2009. Scatter hoarding by the Central American agouti: a test of optimal cache spacing theory. *Animal Behaviour*, **78**, 1327-1333.

Gill, B.J. (convener); Bell, B.D.; Chambers, G.K.; Medway, D.G.; Palma, R.L.; Scofield, R.P.; Tennyson, A.J.D.; Worthy, T. 2010. Checklist of the birds of New Zealand, Norfolk and Macquarie islands, and the Ross Dependency, Antarctica. Fourth Edition. Te Papa Press, Wellington, New Zealand.

Hunt, S., Low, J. & Burns, K. C. 2008. Adaptive numerical competency in a food-hoarding songbird. *Proceedings of the Royal Society B: Biological Sciences*, **275**, 2373-2379.

Kaspari, M. 1990. Prey preparation and the determinants of handling time. *Animal Behaviour*, **40**, 118-126.

Leaver, L. A. 2004. Effects of food value, predation risk, and pilferage on the caching decisions of *Dipodomys merriami*. *Behavioral Ecology*, **15**, 729-734.

Lima, S. L. 1986. Predation risk and unpredictable feeding conditions: determinants of body mass in birds. *Ecology*, **67**, 377-385.

Jansen, P. A. & Forget, P. M. 2001. Scatterhoarding and tree regeneration. *Dynamics and plant-animal interactions in a Neo- tropical rainforest*, 275-288. Kluwer Academic Publishers, Dor- drecht, The Netherlands.

Jansen, P. A., Bartholomeus, M., Bongers, F., Elzinga, J. A., Ouden, J., & Wieren,S. E. 2002. The role of seed size in dispersal by a scatter hoarding rodent. *Seed dispersal and frugivory: ecology, evolution, and conservation*, 209-225. CABI Publishing, New York, USA.

Jansen, P. A., Bongers, F. & Hemerik, L. 2004. Seed mass and mast seeding enhance dispersal by a neotropical scatter-hoarding rodent. *Ecological Monographs*, **74**, 569-589.

Mackintosh, M. A. & Briskie, J. V. 2005. High levels of hatching failure in an insular population of the South Island robin: a consequence of food limitation? *Biological Conservation*, **122**, 409-416.

Maloney, R. F. & McLean, I. G. 1995. Historical and experimental learned predator recognition in free-living New-Zealand robins. *Animal Behaviour*, **50**, 1193-1201.

Marti, C. D. & Hogue, J. G. 1979. Selection of prey by size in screech owls. *The Auk*, **96**, 319-327.

Moles, A. T., Warton, D. I. & Westoby, M. 2003. Do small-seeded species have higher survival through seed predation than large-seeded species? *Ecology*, **84**, 3148-3161.

Powlesland, R. G. 1980. Food storing behaviour of the South Island robin. *Mauri Ora*, **8**, 11-20.

Powlesland, R. G. 1981. The foraging behaviour of the South Island robin. *Notornis*, **28**, 89-102.

Powlesland, R. G. 1983. Breeding and mortality of the South Island robin. *Notornis*, **30**, 265-282.

Pyke, G. H., Pulliam, H. R. & Charnov, E. L. 1977. Optimal foraging: a selective review of theory and tests. *The Quarterly Review of Biology*, **52**, 137-154.

Quinney, T. E. & Ankney, C. D. 1985. Prey size selection by tree swallows. *The Auk*, **102**, 245-250.

Rincón, P. A. & Lobón-Cerviá, J. 1999. Prey-size selection by brown trout (*Salmo trutta L.*) in a stream in northern Spain. *Canadian Journal of Zoology*, **77**, 755-765.

Sherry, T. W. & McDade, L. A. 1982. Prey selection and handling in two neotropical hover-gleaning birds. *Ecology*, **63**, 1016-1028.

Stapanian, M. A. & Smith, C. C. 1978. A model for seed scatterhoarding: coevolution of fox squirrels and black walnuts. *Ecology*, **59**, 884-896.

Steer, J. 2006. Seasonality of food use and caching in New Zealand robins (*Petroica australis*). MSc thesis, Victoria, University of Wellington.

Steer, J. & Burns, K. C. 2008. Seasonal variation in male-female competition, cooperation and selfish hoarding in a monogamous songbird. *Behavioral Ecology and Sociobiology*, **62**, 1175-1183.

Stephens, D. W. & Krebs, J. R. 1986. Foraging theory. Princeton University Press, Princeton, New Jersey, USA.

Towns, D. R. & Daugherty, C. H. 1994. Patterns of range contractions and extinctions in the New Zealand herpetofauna following human colonisation. *New Zealand Journal of Zoology*, **21**, 325-339.

Uller, C., Jaeger, R., Guidry, G. & Martin, C. 2003. Salamanders (*Plethodon cinereus*) go for more: rudiments of number in an amphibian. *Animal Cognition*, **6**, 105-112.

van Horik, J. & Burns, K. C. 2007. Cache spacing patterns and reciprocal cache theft in New Zealand robins. *Animal Behaviour*, **73**, 1043-1049.

Vander Wall, S. B. 1995. The effects of seed value on the caching behavior of yellow pine chipmunks. *Oikos*, **74**, 533-537.

Vander Wall, S. B. & Jenkins, S. H. 2003. Reciprocal pilferage and the evolution of food-hoarding behavior. *Behavioral Ecology*, **14**, 656-667.

Waite, T. A. 1992. Social hoarding and a load size-distance relationship in gray jays. *The Condor*, **94**, 995-998.

Waite, T. A. & Reeve, J. D. 1992. Caching behaviour in the gray jay and the source-departure decision for rate-maximizing scatterhoarders. *Behaviour*, **120**, 51-68.

Wang, B. & Chen, J. 2009. Seed size, more than nutrient or tannin content, affects seed caching behavior of a common genus of Old World rodents. *Ecology*, **90**, 3023-3032.

Werner, E. E. & Hall, D. J. 1974. Optimal foraging and the size selection of prey by the bluegill sunfish (*Lepomis macrochirus*). *Ecology*, **55**, 1042-1052.

Worthy, T. H. & Holdaway, R. N. 2002. The lost world of the moa: prehistoric life of New Zealand. Indiana University Press, Indiana, USA.

Xiao, Z., Zhang, Z. & Wang, Y. 2004. Dispersal and germination of big and small nuts of *Quercus serrata* in a subtropical broad-leaved evergreen forest. *Forest Ecology and Management*, **195**, 141-150.

Xiao, Z., Zhang, Z. & Wang, Y. 2005. Effects of seed size on dispersal distance in five rodent-dispersed fagaceous species. *Acta Oecologica*, **28**, 221-229.

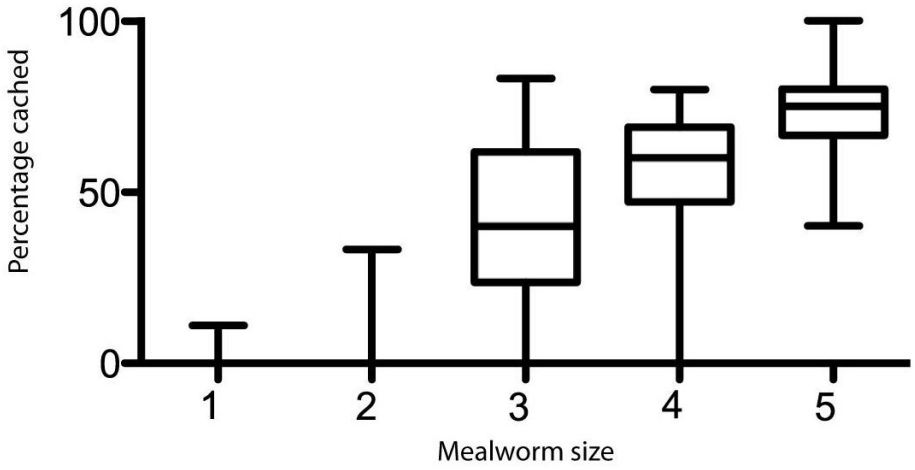

Figure 2.1. Variation in the percentage of mealworms cached across different sizes of mealworm prey.

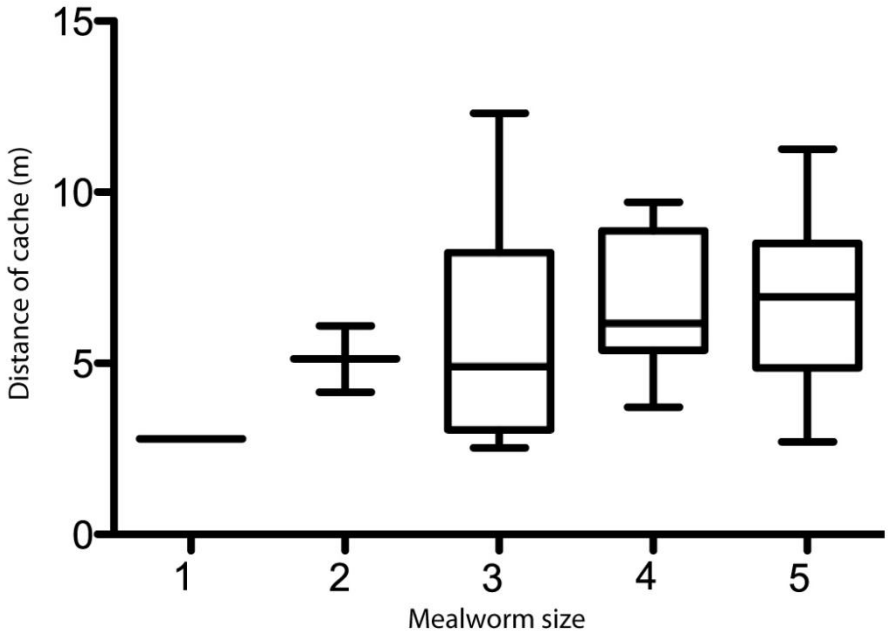

Figure 2.2. Variation in the distance mealworms were cached across different sizes of mealworm prey.

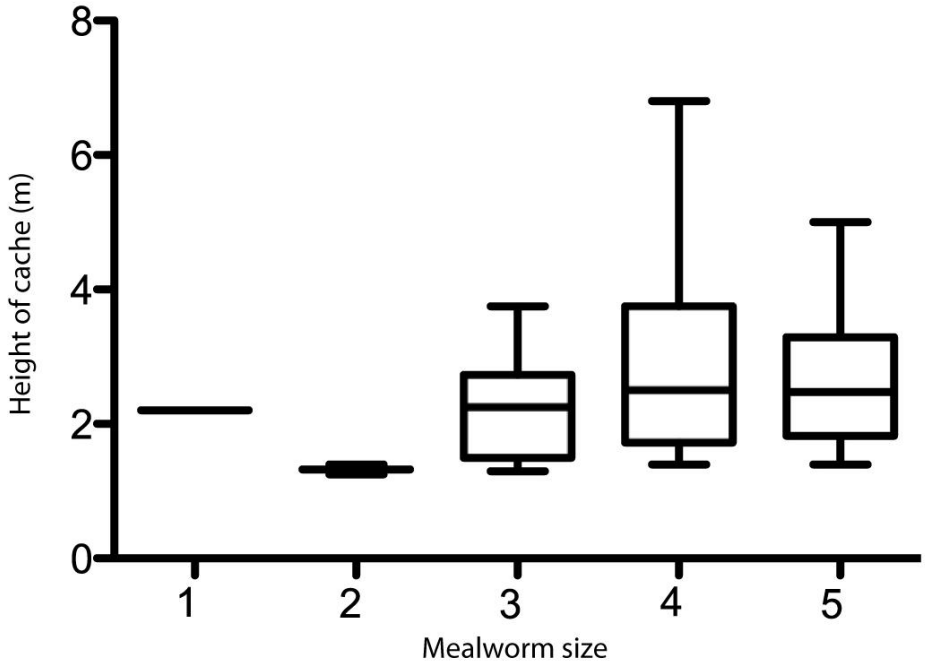

Figure 2.3. Variation in the height mealworms were cached across different sizes of mealworm prey.

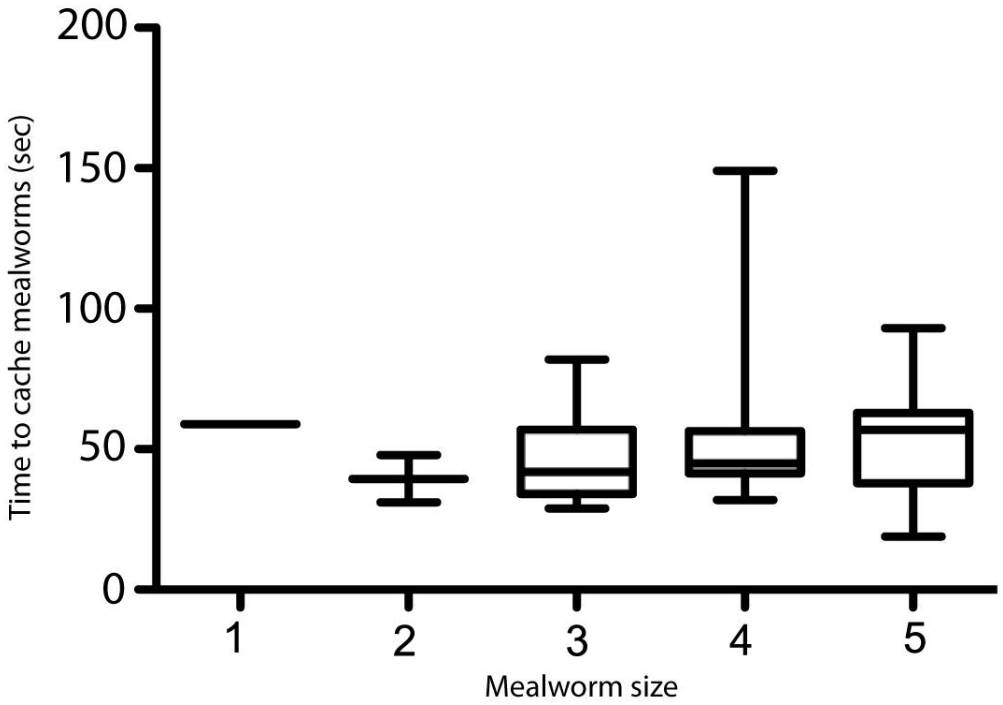

Figure 2.4. Variation in the time taken to cache mealworms across different sizes of mealworm prey.

CHAPTER 3

Pilfering and caching behaviour in the South Island robin (*Petroica australis australis*)

3.1 Abstract. – Caching food provides many benefits but it also leaves food vulnerable to pilferers. However, animals have evolved many strategies to avoid cache loss. Although pilfering is costly to the storer, this may be reduced if theft is reciprocal. For example, New Zealand robins form pair bonds and pairs often pilfer each other's caches, but this behaviour is reciprocal and may benefit both individuals. Robins also pilfer the caches of neighbouring birds and it is expected that cachers will adjust their behaviour to prevent or reduce pilfering. I tested if South Island robins respond to experimental pilfering by changing their future caching behaviour. I fed robins sufficient mealworms to create 10 caches and then removed the mealworms from the 3 nearest caches to the feeding circle. The next day, I fed the same birds a sufficient number of mealworms to create 10 new caches and compared differences in their caching behaviour between the two days. I found that robins on the second day (after experimental pilfering) cached food further away and more often out of sight than on the first day (before experimental pilfering). There was also a weak trend for caches on the second day to be placed higher in trees and for birds to consume more food rather than caching it. The response of the robins to experimental pilfering suggests they respond to the loss of their caches by altering subsequent cache locations. By caching further away, higher up, out-of-view, and consuming food appear to function to reduce cache theft. Robins may have evolved these behaviours to protect their caches from rival birds although it is not clear if they are also trying to protect caches from their mate.

3.2 Introduction

It is not unusual for conspecifics to forage side-by-side in the same habitat; however, when it comes to caching food, an individual animal usually appears to do it discreetly or secretively and in locations away from other individuals and their caches (James & Verbeek, 1983; Hampton and Sherry 1994). Both conspecifics and other animals are well known to pilfer the caches of other individuals. As a result, it is thought that solitary behaviour while caching is a selfish strategy to reduce pilfering and to favour recovery by the caching animal. This is referred to as the "selfish hoarding hypothesis" (Anderson & Krebs 1978; Stapanian & Smith 1978). For caching to evolve, pilfering would need to have been kept below a minimum level to ensure the benefits of the recovered caches more than compensates for any loss (Briggs & Vander Wall 2004; Smulders 1998). If a large proportion of caches are pilfered in certain locations or types of sites, selection should favour a change in caching behaviour to reduce the level of pilfering. On the other hand, pilfering behaviour is also expected to evolve if stealing food from caches provides a higher payoff for the pilfering animal than foraging for its own food. Eckman (1989) found that for caching to be evolutionary stable among tits (Family Paridae), it is essential for caching animals to consume more of their cached food than their pilferers consume. In other words, a caching individual must have a "recovery advantage". If pilfering is above this level, caching would be maladaptive and the behaviour to be selected against.

To prevent pilfering, caching animals implement a number of behavioural strategies that appear to reduce the likelihood that thieves will steal their caches (Dally *et al.* 2006). Perhaps the most common protection mechanisms are to cache in ways that discourage pilfering. For example, Merriam's kangaroo rats (*Dipodomys merriami*) change the density of their cache sites so that they are at an 'optimal density' (Jenkins *et al.* 1995).

They initially hoard seeds close to the seed source, possibly to maximise the harvest rate during flushes of seed production and to make seeds unavailable to competitors. Then as food sources are diminished, they begin to distribute caches more evenly among caching compartments. Changing cache density to reduce pilfering is also a mechanism used by some birds living in flocks and family units with hierarchies (James and Verbeek 1983). Socially subordinate birds such as willow tits (*Parus montanus*), which cannot defend their caches, instead hoard in a large number of widely scattered cache sites with only a small amount of food in each one (Lahti *et al.* 1998). The degree to which food is scatter hoarded makes random searching for caches by dominant birds less productive and reduces the proportional loss if a cache is encountered and pilfered. Conversely, dominant animals may benefit from larder hoarding, or caching large amounts of food in a small number of spatially aggregated sites, which can be more easily defended (Ekman 1989). However, some studies have found that competition for cache retrieval does not affect food hoarding intensity (e.g., Burns 2009). Patterns in cache retrieval suggest that differences in cache spacing do not reduce the likelihood of cache theft, and other processes such as mate provisioning may be important (van Horik & Burns 2007).

Clarkson *et al.* (1986) found that magpies (*Pica pica*) change the density of their cache sites with the strength of density-dependent cache loss. Food that is hidden close to the source may be found easily by others, yet if hoarded further afield, a lot of time will be spent by the caching animal in travel. The individuals that best balance energy gains with travel time should be on average fitter than individuals that waste time and cache in a manner that results in the retrieval of only a few items of value. If a caching individual learnt that some locations were more prone to being pilfered and avoided caching in them, then they would be expected to have a recovery advantage over and above individuals that

do not adjust the locations they choose for caching. Being able to learn from cache loss may create extra selective pressures for increased memory capacity in food-storing birds beyond that required for remembering and relocating cache sites alone.

Although many caching animals change their behaviour in the presence of competitors, a few studies on titmice in the Family Paridae have shown that they may further assess the level of competition around them. In other words, animals may be able to directly determine the level of competition from the percentage of their caches that have been pilfered. Marsh tits (*Parus palustris*) increased caching in locations where their seeds had not been removed (Sherry *et al.* 1982), while black-capped chickadees (*Poecile atricapillus*) learned to avoid caching in spatial locations where previous caches were lost and reduced search times for caches in risky locations (Hampton & Sherry 1994). On the other hand, caching individuals may indirectly assess competition from the number of possible pilferers in their environment. When willow tits were foraging alone they cached closer to the feeder (Lahti *et al.* 1998). Similarly, black-capped chickadees cached more often when they were alone (Stone & Baker 1989).

Other strategies to avoid pilfering include the cessation of caching and actively defending caches. Carrascal & Moreno (1993) found nuthatches (*Sitta europaea*) ate a greater proportion of husked peanuts when in the presence of another individual, compared with solitary nuthatches which hoarded proportionately more. The opposite was demonstrated for deer mice (*Peromyscus* spp.) which cached proportionately more food when in presence of conspecifics (Sanchez & Reichman 1987). It was suggested that the increase of caching in the presence of conspecifics made sense if caches could be actively defended against theft (Sanchez & Reichman 1987). Eastern chipmunks (*Tamias striatus*) chase competitors away and prevent access to their cache sites (Clarke & Kramer 1994). A

number of authors have observed male New Zealand robins (*Petroica australis*) aggressively defend caches and attack their partners whenever they approached experimental food sources (Alexander *et al.* 2005; Burns & Steer 2006; van Horik & Burns 2007).

To reduce pilfering, many caching animals may try to prevent animals knowing the location of their cache sites. Bugnyar & Kotrschal (2002) found common ravens (*Corvus corax*) which were approached by potential thieves, in all cases interrupted the behavioural sequence of caching and cached in another site. Several studies have found corvids and parids cache 'out-of-view' of competitors. For example, Western scrub-jays (*Aphelocoma californica*) cache in predominantly out-of-view sites compared with equidistant in-view sites when being observed (Dally *et al.* 2005a). Western scrub-jays also repeatedly moved caches around and cached in hard-to-see sites that were in shade rather than well-lit areas when being watched by an observer (Dally *et al.* 2004; Dally *et al.* 2005a; Dally *et al.* 2005b). Emery & Clayton (2001) also found scrub jays (*A. coerulescens*) re-cached food items once the observer had left.

If pilfering does occur, then it would be advantageous for a caching individual to alter its caching behaviour to reduce the risk of further cache loss. For example, ravens and scrub jays avoid caching in the presence of potential thieves (Emery & Clayton 2001, Dally *et al.* 2005b). Black-capped chickadees make false caches, whereby they place a food item in a cache site and immediately pick it up and take it in another site, supposedly leaving the impression on watching conspecifics that the food is still in the first cache site (Stone & Baker 1989). Other animals hoard food in habitats that enhance the probability of cache retrieval (Briggs & Vander Wall 2004; Dally *et al.* 2004). Corvids retrieve and then re-cache previously cached prey, they use observational learning

to pilfer caches and re-cache hoards when potential thieves are preoccupied (Emery & Clayton 2001; Emery *et al.* 2004; Dally *et al.* 2005b). Furthermore, ravens will cache behind large objects in the presence of conspecifics. These objects may serve as barriers concealing information about the location of caches from potential thieves (Bugnyar & Kotrschal 2002). Dally *et al.* (2005a) found that when an observer is always present at the time of caching, jays use distance and barriers to reduce the probability of cache theft by conspecifics. Most caching animals will use multiple strategies to give them a recovery advantage over their would-be-pilferers (Dally *et al.* 2006).

Although pilfering in many cases is likely to incur a cost to the caching animal, the cost of pilfering can be reduced and evolutionarily stable through reciprocal cache theft among unrelated individuals and through the inclusive fitness benefit by sharing with closely related family members (Vander Wall & Jenkins 2003). Reciprocal cache theft may also be the case for New Zealand robins; male and female robins regularly pilfer their partner's cached mealworms. Robins are unlike many other passerine species, in that they form pair bonds that last for multiple years and male robins are almost always the biological father of their offspring (Taylor *et al.* 2008). Extra-pair paternity may be low in robins because they are relatively long lived and have obligatory parental care (Taylor *et al.* 2008). Because of the inclusive fitness that the robin parents gain through their offspring, it is expected that pilfering may be tolerated to a degree by either sex if it were to benefit their offspring. However, if a non-kin individual was to do the pilfering, one might predict that robins will adjust their caching behaviour to reduce cache theft. In this chapter, I test whether New Zealand robins alter their caching behaviour in response to the experimental pilfering of their caches by a non-kin individual.

3.3 Methods

Study site and species

For a complete description of the field sites and study species refer to Chapter 2.

Field experiment

Robins readily approach humans in the wild and cache hand-fed mealworms. I conducted two trials on each male robin (n = 12) on consecutive days. All birds were identified by permanent leg bands and sexes were confirmed with banding records. In the summer of 2009/2010 almost all the robins were banded at both field sites. Trials were conducted between 9 am and 4 pm and were halted if interrupted by strong winds or moderate to heavy rainfall. Juveniles, whose sex is difficult to identify, were excluded from trials.

Robins were first located by sight or by their song. To attract robins to within a few metres, I used either clapping, singing, and pishing sounds, or by hitting broken branches against trees. In all cases, these noises attracted robins to my immediate vicinity. I also cleared a circular area of ground about 75 cm diameter of all dead leaves and ferns to use as the feeding point. I stood approximately 2 m from the feeding point during trials. Robins are attracted to disturbed ground, perhaps to feed on the invertebrates uncovered. The experiments were only started when the males were accompanied by their partner in the nearby vicinity. When the male robin was within 4 m, I began the trial by throwing a mealworm into the centre of the feeding point. Prior to the experiments, I weighed each mealworms (to 0.001 g) on a Ohaus Scout Pro Portable scale. The mealworms weighed between 0.120g and 0.180g. I wanted to use similar sized mealworms because I thought that robins may change their caching behaviour depending on the size of the prey item and

it would increase variation in my results. I conducted trials on only male robins, however, they were always accompanied by their mate at the start of trials. Sometimes a rival male showed up at the trial; this interaction would usually result in one male chasing the other off. If the male did not return after 5 minutes then the trial was started again the following day. Most birds consumed 5 to 10 mealworms before caching in nearby trees. A mealworm was defined as cached if it was transported in a robin's bill and deposited in a new location.

Mealworms were thrown to the robins one at a time, and each mealworm was randomly selected each time from a container. The next mealworm was fed to the robin once the previous one had been eaten or the robin had returned after caching. I fed the robins mealworms up until they had cached a total of 10 worms. Immediately after I had finished feeding the robins I pilfered the three closest cached mealworms (in terms of distance). On occasion, the 2 or 3 of the closest cached mealworms occurred in the same cache; in this situation all were counted independently. If the mealworm had already been eaten by the male, re-cached or pilfered I then went to the next closest cache to pilfer a worm. I went to the same location on the second day to repeat the feeding experiment. If a male robin failed to show up then the whole experiment was repeated again another day. In most cases (10/12 birds) the robin would show up the day after I pilfered the caches, and mealworms were fed to the robin until he had cached another 10 mealworms.

Statistical analysis

I quantified three dependent variables to characterize the effort (time + energy) spent caching a mealworm. First, the time was recorded from when the robin picked the

mealworm up in its bill to when it flew away from the feeding circle. I measured the height and distance of caches after the trial was complete. I did not measure the location of caches until the trial was complete to avoid disturbing caches and thereby potentially changing the behaviour of the birds. To remember locations of caches during the trial, I noted the direction, height, distance, tree species and any defining characteristics of the cache in a notebook. I was not successful in relocating all the caches after the trial was complete, as caches made out-of-sight were difficult to find. However, I was able to locate 62% of caches on the first day of the experiments and 50% on the second day. Both distance and height were measured with a measuring tape. Distance was measured as the distance between the experimental food source (i.e., the location on the forest floor where the mealworms were placed) and the point on the ground below the cache site. Height was measured as the distance between the cache site and the point directly below on the forest floor. I also tested two qualitative variables: whether caching occurred out-of-sight, and whether food was consumed immediately. D'Agostino & Pearson omnibus normality tests were used on all data to test for normality. Height, time and whether eaten were all non-normal and Wilcoxon matched-pairs signed rank tests were used to test this non-parametric data. Length and cached out-of-sight were normally distributed and paired t-tests were used to test data.

3.4 Results

Robins were significantly more likely to cache mealworms out of my view ($t = 3.02$, $p = 0.01$) after I have pilfered caches on the first day. Before pilferage, robins cached an average of 4.91 (s.d. = 2.19) mealworms out-of-sight and after pilferage they cached 6.58 (s.d. = 2.28) mealworms out of sight (Figure 3.1). Robins also tended to eat more

mealworms after experimental pilfering than before but the difference was not significant (Figure 3.2; T = -29.00, p = 0.10).

The location of caches differed between the first day and the second day of my experiment. Robins cached mealworms significantly further away from the feeding circle after pilfering than before pilfering (Figure 3.3; T-value = 2.28, p = 0.04). The average distance robins cached mealworms before pilfering was 5.54 m (s.d. = 1.37 m) and 6.88 m (s.d. = 1.38 m) after pilfering. However, there was no significant difference between the height mealworms were cached in experiments before and after pilfering (Figure 3.4; T = -42.00, p = 0.11). The average height robins cached mealworms before pilfering was 3.04 m (s.d. = 0.72 m) and 3.44 m (s.d. = 0.85 m) after pilfering.

The time taken to cache mealworms did not differ before and after pilfering (Figure 3.5; T = - 14.00, p = 0.61). On average, robins took longer to cache mealworms after pilfering, 0.47 seconds before pilfering and 0.55 seconds after pilfering, however variation was very high, s.d = 0.24 seconds and s.d. = 0.34 seconds, respectively.

3.5 Discussion

My study indicates that robins are sensitive to their social environment, and use this information when making caching decisions. They changed their caching strategy after I pilfered their caches, placing caches further away from the feeding point and were more likely to cache prey out-of-sight. Robins also tended to eat more mealworms and place caches higher up after experimental cache pilfering. Although I predicted robins would take longer to cache mealworms because it should take longer to fly further away and return, my results did not show this was the case. Nevertheless, taken together my results

clearly demonstrate that robins created new caches after an episode of pilfering in a manner that should reduce the chances of these new caches being pilfered.

There is some experimental evidence that supports the idea that animals change caching in the presence of a competitor. For example, willow tits cache closer to the feeder when alone than in the presence of conspecifics (Lahti *et al.* 1998). These effects of competitor presence on caching may be due to the fact that cache observation facilitates pilferage (Preston & Jacobs 2001). In experiments with Pinyon jay (*Gymnorhinus cyanocephalus*), observer jays often remember the area of their partner's cache (Bednekoff & Balda 1996). Many birds and mammals abort caching in the presence of potential thieves (Steller's jays, *Cyanocitta stelleri,* Burnell & Tomback 1985; northwestern crow, James & Verbeek 1993; grey squirrels, *Sciurus carolinensis,* Steele *et al.* 2008), which are also known to pilfer caches. The change in the behaviour of robins in response to my experimental pilfering of their caches, suggests they likewise viewed me as a potential pilferer and in my presence, altered the locations of their subsequent caches.

In my experiment, I removed the three closest existing caches to the feeding point, providing the robins with spatial information on where to cache and where not to cache. After experiencing cache loss, the robins placed caches in a way that agreed with my predictions and reflected the pattern of cache loss. This ability of robins to react in such a way may be an important behaviour in the wild because pilfering the caches of other individuals is common among New Zealand robins (van Horik & Burns 2007) and other caching animals (magpie, *Pica pica,* Clarkson *et al.* 1986; northwestern crow, James & Verbeek 1983; gray jay, *Perisoreus canadensis,* Waite 1988). Individuals that cache in sites that experience a low overall rate of pilfering should be able to retrieve more of their caches than an animal that does not change their caching behaviour in the face of

systematic cache loss. Scatter hoarders must relocate food from a number of spatially distributed cache sites which has probably led to the selective enhancement of some properties of memory in caching birds (Krebs *et al.* 1989; Shettleworth 1990). The ability of learning about cache loss may produce additional selective pressure for memory in caching birds (Hampton & Sherry 1994).

Male robins transported mealworms to more distant cache sites and were significantly more likely to be out-of-view (behind trees, branches and other vegetation) from where I was standing during experiments. Because they can change their food hoarding behaviour in response to a novel pilferer, robins gain a recovery advantage and this ability may be important for caching behaviour to evolve (Andersson & Krebs 1978; Vander Wall & Jenkins 2003). The change in caching behaviour on the second day of my experiment suggests that robins may have been attempting to hide their cached food from me. In other words, secrecy appears to be an important behaviour for protecting their caches from pilferage. As a consequence of trying to conceal their cached food, mealworms were also placed further away from the feeding point. However, mealworms may have been out-of-view because robins were trying to put more space between me and their caches as a consequence of my pilferage of only the three nearest mealworms. From these results I cannot be sure whether out-of-view or distance was the most important protection strategy from a robin's perspective, but a combination of the two strategies is also possible. In this experiment, robins had the opportunity to learn where not to cache mealworms, but it would be interesting to know if robins also learn to preferentially check cache sites that are unlikely to have been pilfered. I expect that robins would preferentially check those cache sites furthest away and out-of-view because those sites are unlikely to have been pilfered. Robins should behave in this way because many pilferers rely on

seeing the caching animal cache the food to relocate cache sites successfully. If they did not see the storer making the cache site, they would need to rely on random searching which is likely a less effective method for pilfering the caches of other individuals.

Although robins flew further away to cache mealworms on the second day of my experiment, they did not take longer to travel to more distant cache sites as I had expected. If robins were to take longer to cache mealworms, you would expect energy expenditure to be greater because they are putting more effort into caching. But it is in an animal's best interest to not expend energy if possible, unless there are benefits from doing so. My prediction was based on past research by Carrascal & Moreno (1993); they found nuthatches (*Sitta europaea*) spent more time travelling when accompanied by a conspecific during caching. They suggest that they may use the behaviour to discourage other conspecifics following and in turn being able to see the cache location. If their hypothesis is correct, it is possible that robins did not spend longer caching because I never followed them while they were caching. On the other hand, if I had moved closer or around obstacles I may not have been out-of-sight so many times while they cached and I would not have been able to estimate the effect of my presence on the locations of their new caches.

Whether flying further or out of sight substantially increases the costs of caching are not clear. When you consider how fast birds can move amongst the trees, it would also be easy for birds to cache only a little further away from the feeding point without spending much more time travelling, and yet as a result, be obscured from my view. When I observed robins caching during the experiment, much time was spent perched at the cache site, on nearby branches and flying around in the close vicinity. I suggest the large amount of individual variation in the time taken while caching is due to the time robins

spent when they were not actively caching food but performing other behaviours before returning to the feeding point. These other behaviours may include territorial defence, searching for their mate and/or offspring and possibly secretively re-caching mealworms. In this case, if they did spend more time purely caching the mealworm, it was not picked up by my experiment.

Perhaps robins can cache food farther away without spending more time doing so because they fly faster. Heinrich & Pepper (1998) found ravens cache food more quickly when the risk of losing it to competitors is greater. Robins may associate me with being feed, therefore they may return quickly to me after caching so that they make the most of the large and easy supply of food. Heinrich & Pepper (1998) found that when presented with food that could easily be removed by one bird in relatively quick successive trips the birds greatly increased their caching speed. In contrast, when they presented a small quantity of food that one bird could easily control, the birds delayed caching. These results indicate that the ravens' immediate goal of caching was to maximise the amount of food removed from the competition. Another possibility is because robins were only fed one mealworm at a time, they may appear to take a long time to cache because they are performing other tasks before returning to the feeding circle to continue the experiment. In either case, measuring flight speeds and time of each activity involved with caching might be able to help answer this question.

Rooks (*Corvus frugilegus*, Goodwin 1986) and scrub-jays (Dally *et al.* 2005a) successfully use aggressive acts to discourage would-be pilferers from cache sites. Whilst aggressive defence is an effective cache protection tactic in dominant birds, it is also an energetically expensive and potentially dangerous one. Injuries sustained during an aggressive interaction can result in fatalities for both combatants, not only for the would-

be thief. By repeatedly moving items around, however, caching individuals might reduce the accuracy with which competitors are able to use observational spatial memory to facilitate cache theft, and therefore the need for aggressive cache defence, as memory for the location of the prior cache sites might interfere with the memory for current cache location. Dally *et al.* (2005a) have shown that moving caches around does not affect the accuracy with which storers are able to recover their own caches. It would be interesting to know if robins moved more caches around more often on the day after pilferage than they did the day before pilfering took place.

The ability to differentiate between observers that do and do not pose a risk to cache safety represents a clear advantage to caching individuals. In ravens and scrub-jays there is evidence that storers do not use cache protection strategies if their partner is the only witness to a caching event and they are not prevented from accessing the storer's cache sites (Dally *et al.* 2005a; Heinrich & Pepper 1998). These findings suggest that, at least in ravens (Wilmore 1977) and scrub-jays (Curry *et al.* 2002) that form long-term pair bonds, cachers do not appear to perceive their partner as a threat to cache safety. As female robins often pilfer the caches of their mates, it would be interesting to determine whether males alter their subsequent caching behaviour to mate pilferage in a manner similar to that observed when their caches were pilfered by non-kin (i.e., by me). If pilfering by mates has benefits in terms of inclusive fitness, then one might expect less effect of pilfering by a mate than by non-kin.

I found that there was no difference in the number of cache sites created by robins when before and after pilferage was compared. Other studies have shown that when food-hoarding animals experience pilfering they scatter their cache sites over a wider area. Although the robins after pilferage moved their caches further away, they did not increase

the number of cache sites they made by only placing one mealworm in each cache site. This result is not surprising because South Island robins rarely placed sequential prey in the same site as the previous cached mealworm and during experiments they mostly used cache sites only once.

One behaviour that is sometimes suggested as evidence that non-human animals can plan for the future is caching (Roberts 2002). On the other hand, caching may not be the animal intending to provide food for its self in the future, but rather caching is a genetically programmed species-specific behavioural tendency (Roberts 2002). There are a number of studies trying to resolve the issue around future planning and theory of mind (TOM). For example, Emery & Clayton (2001) found that western scrub-jays can relate their previous experience of pilfering another bird's caches to the possibility of future cache theft by another bird. They re-cached food in new sites, but only when they had been observed during caching (Emery & Clayton 2001). Although these results suggest that scrub-jays are capable of future planning, the degree to which these birds act independently of their current motivational state is a matter of contention (Correia *et al.* 2007). Western scrub-jays do show some ability to act independently of their current motivational state by caching food in a place in which they know they will be hungry in the following morning, and also by storing certain foods in a place in which they know that that food will not be in the following morning (Raby *et al.* 2007). TOM and future planning is very topical and interesting to scientists due to the fact that similar cognitive abilities may be found in species other than humans. However, the Bishof-Kohler hypothesis states that "nonhuman animals are bound to their present motivational state and cannot anticipate or take appropriate action toward the satisfaction of a need or

motivational state that is not currently experienced" and there is still no irrefutable evidence (Suddendorf & Corballis 2008).

Conclusions

The work here shows that robins change their caching behaviour after experiencing experimental cache pilferage. After pilfering robins cached mealworms further away, at lower density and out-of-site from the human observer. If a would-be pilferer does not see a cache being made, the probability that the pilferer searches and randomly finds the cache is low. If food items are cached more remotely, pilferers must cover more ground to find caches. Eating more mealworms immediately rather than caching them and height of cache sites after pilfering were both almost significant. I am confident that they are reliable relationships. Like placing caches further away and at lower density, the height of a cache would also make it more difficult for pilferers by increasing the volume of space they must search. Eating more food means more energy is stored internally and not externally as caches which risk being stolen. Animals react strongly to pilfering because wasting time and energy and losing food is expected to reduce an individuals fitness, thus, preventing pilfering is naturally selected for. As a result of pilfering, I have found a strong reaction from robins.

3.6 Literature cited

Alexander, L., Duthie, C., Fyfe, J., Haws, Z., Hunt, S., Montoya, I., Ochoa, C., Siva, A., Stringer, L., van Horik, J. & Burns, K. C. 2005. An experimental evaluation of food hoarding by North Island robins (*Petroica australis longipes*). *Nortornis*, **52**, 138-142.

Andersson, M. & Krebs, J. 1978. On the evolution of hoarding behaviour. *Animal Behaviour*, **26**, 707-711.

Bednekoff, P. A. & Balda, R. P. 1996. Social caching and observational spatial memory in pinyon jays. *Behaviour*, **133**, 807-826.

Briggs, J. S. & Vander Wall, S. B. 2004. Substrate type affects caching and pilferage of pine seeds by chipmunks. *Behavioral Ecology*, **15**, 666-672.

Bugnyar, T. & Kotrschal, K. 2002. Observational learning and the raiding of food caches in ravens, *Corvus corax*: is it 'tactical' deception? *Animal Behaviour*, **64**, 185-195.

Burnell, K. L. & Tomback, D. F. 1985. Steller's jays steal gray jay caches: field and laboratory observations. *The Auk*, **102**, 417-419.

Burns, K. C. & Steer, J. 2006. Dominance rank influences food hoarding in New Zealand robins *Petroica australis*. *Ibis*, **148**, 266-272.

Burns, K. 2009. Fine-scale food hoarding decisions in New Zealand robins (*Petroica australis*): is inter-sexual competition important? *Journal of Ornithology*, **150**, 321-328.

Carrascal, L. M. & Moreno, E. 1993. Food caching versus immediate consumption in the nuthatch: the effect of social context. *Ardea*, **81**, 135-141.

Clarkson, K., Eden, S. F., Sutherland, W. J. & Houston, A. I. 1986. Density dependence and magpie food hoarding. *Journal of Animal Ecology*, **55**, 111-121.

Correia, S. P. C., Dickinson, A. & Clayton, Nicola S. 2007. Western Scrub-Jays Anticipate Future Needs Independently of Their Current Motivational State. *Current biology : CB*, **17**, 856-861.

Curry, R. L., Townsend Peterson, A. & Langen, T. A. 2002. Western scrub-jay. *The birds of North America*, **712**, 1-35.

Dally, J. M., Emery, N. J. & Clayton, N. S. 2004. Cache protection strategies by western scrub-jays (*Aphelocoma californica*): hiding food in the shade. *Proceedings: Biological Sciences*, **271**, S387-S390.

Dally, J. M., Emery, N. J. & Clayton, N. S. 2005a. Cache protection strategies by western scrub-jays, *Aphelocoma californica*: implications for social cognition. *Animal Behaviour*, **70**, 1251-1263.

Dally, J. M., Emery, N. J. & Clayton, N. S. 2005b. The social suppression of caching in western scrub-jays (*Aphelocoma californica*). *Behaviour*, **142**, 961-977.

Dally, J. M., Clayton, N. S. & Emery, N. J. 2006. The behaviour and evolution of cache protection and pilferage. *Animal Behaviour*, **72**, 13-23.

Ekman, J. 1989. Ecology of non-breeding social systems of Parus. *The Wilson Bulletin*, **101**, 263-288.

Emery, N. J. & Clayton, N. S. 2001. Effects of experience and social context on prospective caching strategies by scrub jays. *Nature*, **414**, 443-446.

Emery, N., Dally, J. & Clayton, N. 2004. Western scrub-jays (*Aphelocoma californica*) use cognitive strategies to protect their caches from thieving conspecifics. *Animal Cognition*, **7**, 37-43.

Goodwin, D. 1986. *Crows of the world, 2nd edition.* British Museum, London, England.

Hampton, R. R. & Sherry, D. F. 1994. The effects of cache loss on choice of cache sites in black-capped chickadees. *Behavioral Ecology*, **5**, 44-50.

Heinrich, B. & Pepper, J. W. 1998. Influence of competitors on caching behaviour in the common raven, *Corvus corax*. *Animal Behaviour*, **56**, 1083-1090.

James, P. C. & Verbeek, N. A. M. 1983. The food storage behaviour of the northwestern crow. *Behaviour*, **85**, 276-291.

Jenkins, S. H., Aron, R. & Green, W. C. H. 1995. Food hoarding by Merriam's kangaroo rats: a test of alternative hypotheses. *Ecology*, **76**, 2470-2481.

Krebs, J. R., Sherry, D. F., Healy, S. D., Perry, V. H. & Vaccarino, A. L. 1989. Hippocampal specialization of food-storing birds. *Proceedings of the National Academy of Sciences*, **86**, 1388-1392.

Lahti, K., Koivula, K., Rytkönen, S., Mustonen, T., Welling, P., Pravosudov, V. V. & Orell, M. 1998. Social influences on food caching in willow tits: a field experiment. *Behavioral Ecology*, **9**, 122-129.

Preston, S. D. & Jacobs, L. F. 2001. Conspecific pilferage but not presence affects Merriam's kangaroo rat cache strategy. *Behavioral Ecology*, **12**, 517-523.

Powlesland, R. G. 1980. Food storing behaviour of the South Island robin. *Mauri Ora*, **8**, 11-20.

Raby, C. R., Alexis, D. M., Dickinson, A. & Clayton, N. S. 2007. Planning for the future by western scrub-jays. *Nature*, **445**, 919-921.

Roberts, W. A. 2002. Are animals stuck in time? ETATS-UNIS: American Psychological Association, Washington, DC, USA.

Sanchez, J. C. & Reichman, O. J. 1987. The effects of conspecifics on caching behavior of *Peromyscus leucopus*. *Journal of Mammalogy*, **68**, 695-697.

Sherry, D., Avery, M. & Stevens, A. 1982. The spacing of stored food by marsh tits. *Zeitschrift für Tierpsychologie*, **58**, 153-162.

Shettleworth, S. J. 1990. Spatial memory in food-storing birds. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, **329**, 143-151.

Smulders, Tom V. 1998. A game theoretical model of the evolution of food hoarding: applications to the Paridae. *The American Naturalist*, **151**, 356-366.

Suddendorf, T. & Corballis, M. C. 2008. New evidence for animal foresight? *Animal Behaviour*, **75**, e1-e3.

Stapanian, M. A. & Smith, C. C. 1978. A model for seed scatterhoarding: coevolution of fox squirrels and black walnuts. *Ecology*, **59**, 884-896.

Steele, M. A., Halkin, S. L., Smallwood, P. D., McKenna, T. J., Mitsopoulos, K. & Beam, M. 2008. Cache protection strategies of a scatter-hoarding rodent: do tree squirrels engage in behavioural deception? *Animal Behaviour*, **75**, 705-714.

Stone, E. R. & Baker, M. C. 1989. The effects of conspecifics on food caching by black-capped chickadees. *The Condor*, **91**, 886-890.

Taylor, S. S., Boessenkool, S. & Jamieson, I. G. 2008. Genetic monogamy in two long-lived New Zealand passerines. *Journal of Avian Biology*, **39**, 579-583.

van Horik, J. & Burns, K. C. 2007. Cache spacing patterns and reciprocal cache theft in New Zealand robins. *Animal Behaviour*, **73**, 1043-1049.

Vander Wall, S. B. & Jenkins, S. H. 2003. Reciprocal pilferage and the evolution of food-hoarding behavior. *Behavioral Ecology*, **14**, 656-667.

Waite, T. A. 1988. A field test of density-dependent survival of simulated gray jay caches. *The Condor*, **90**, 247-249.

Wilmore, S. B. 1977. *Crows, jays, ravens and their relatives.* David & Charles, London, England.

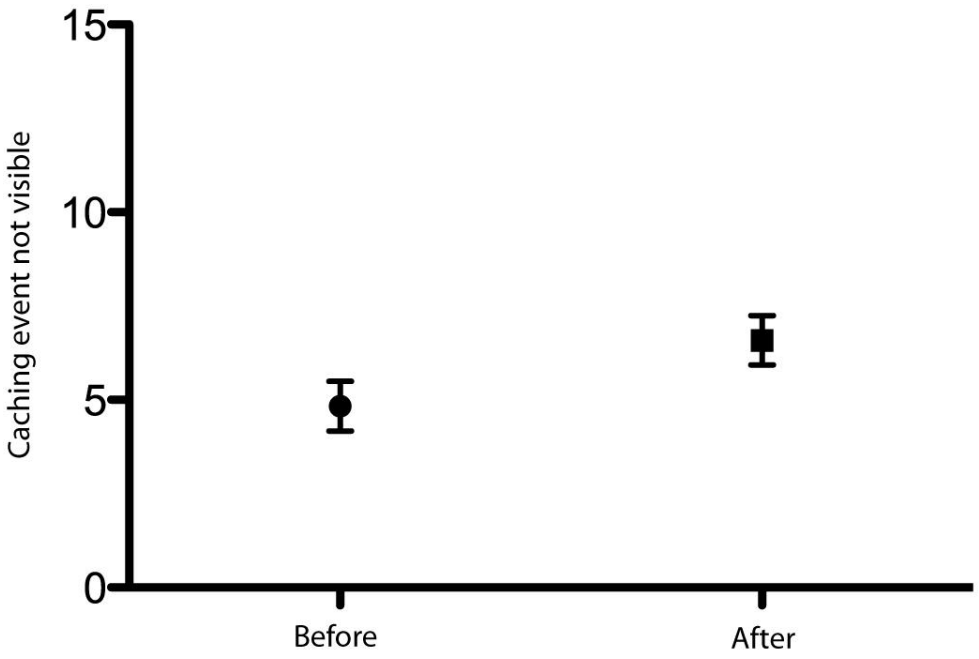

Figure 3.1. The number of caching events not visible to the human observer before and after experimental cache pilfering. Symbols show mean ± SD.

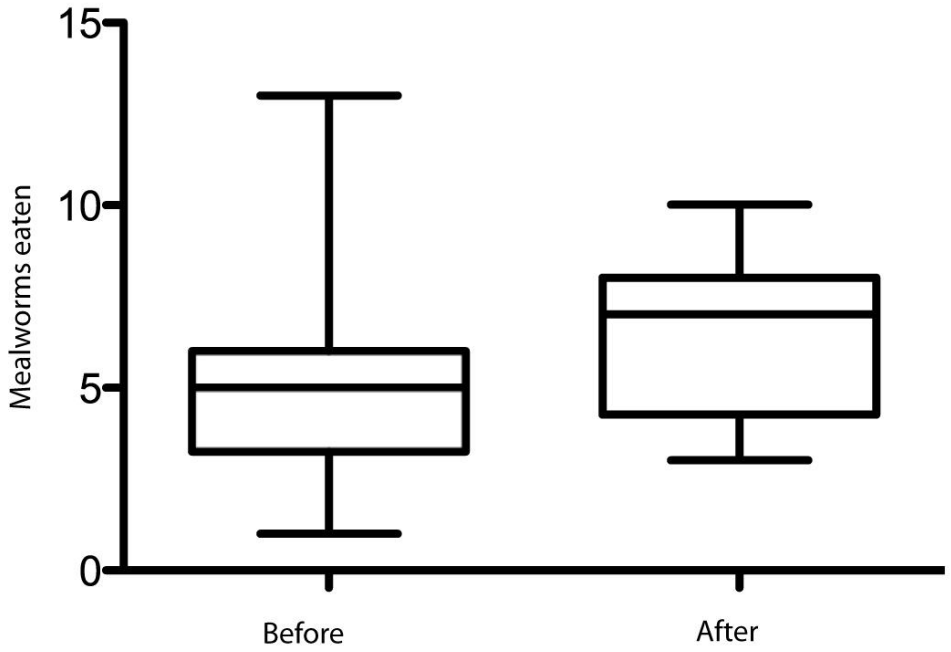

Figure 3.2. The number of mealworms eaten and not cached before and after experimental cache pilfering. Shown are the medians, and 25th and 75th percentiles.

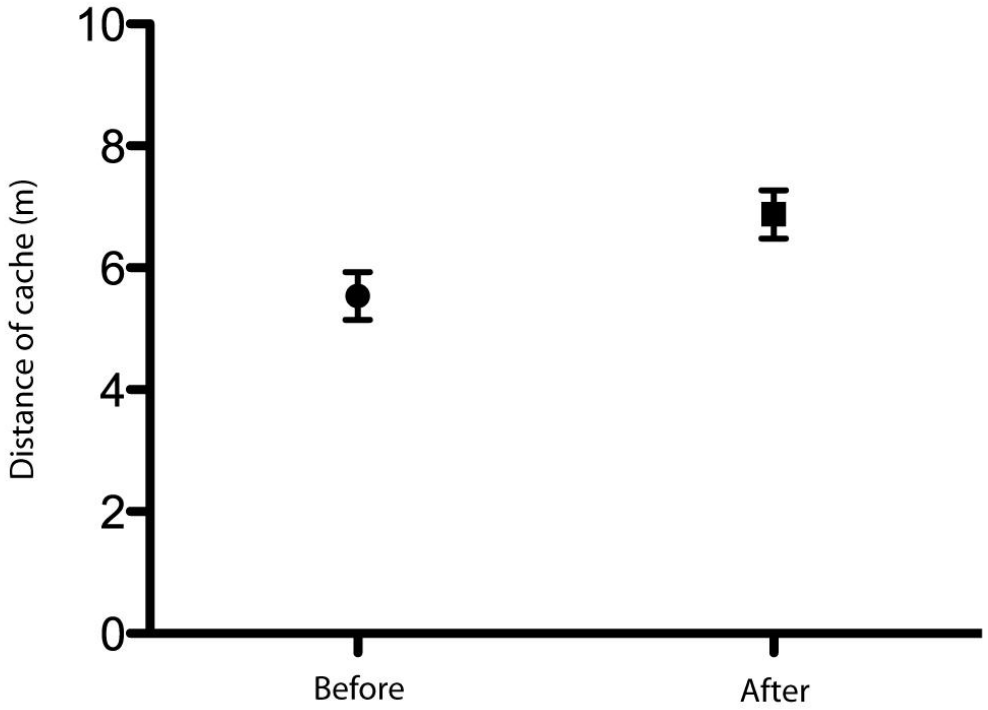

Figure 3.3. The length of the caches from the feeding circle before and after experimental cache pilfering. Symbols show mean ± SD.

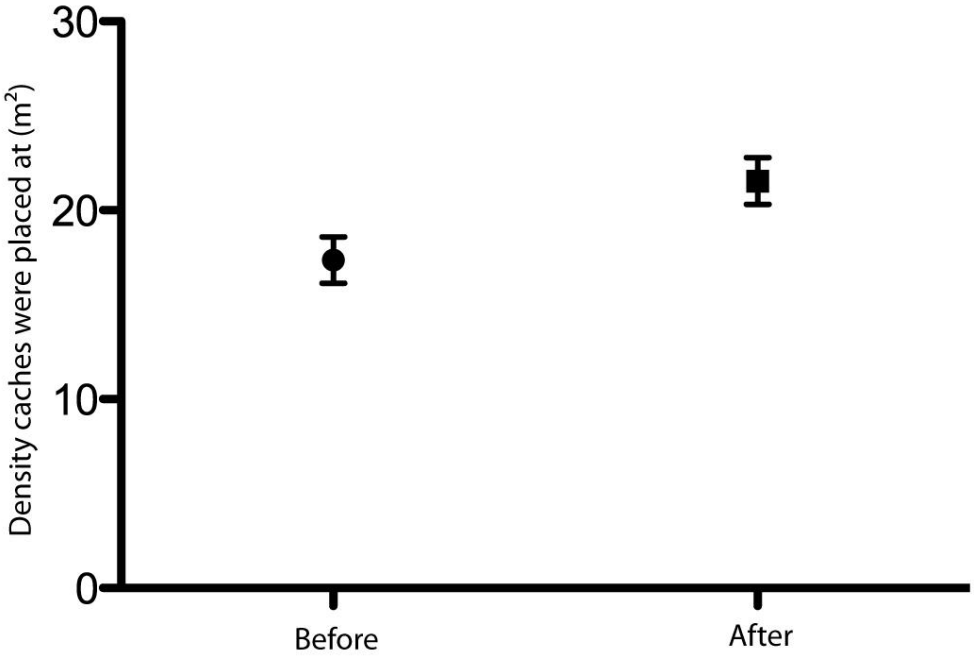

Figure 3.4. The density away from the feeding point that caches were placed at. Symbols show mean ± SD.

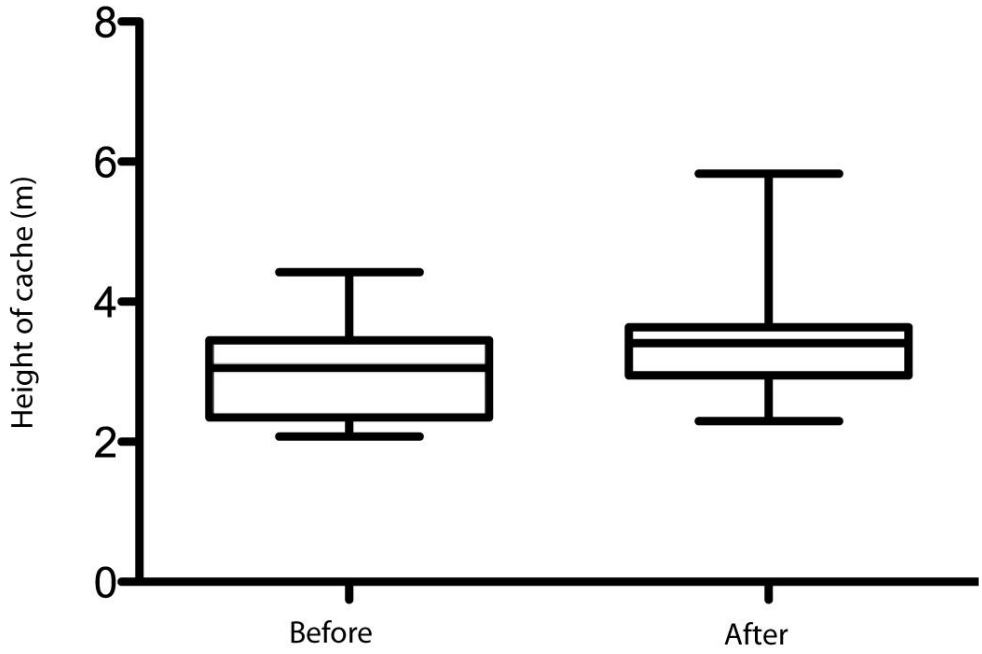

Figure 3.5. The height of the caches off the ground before and after experimental cache pilfering. Shown are the medians, and 25th and 75th percentiles.

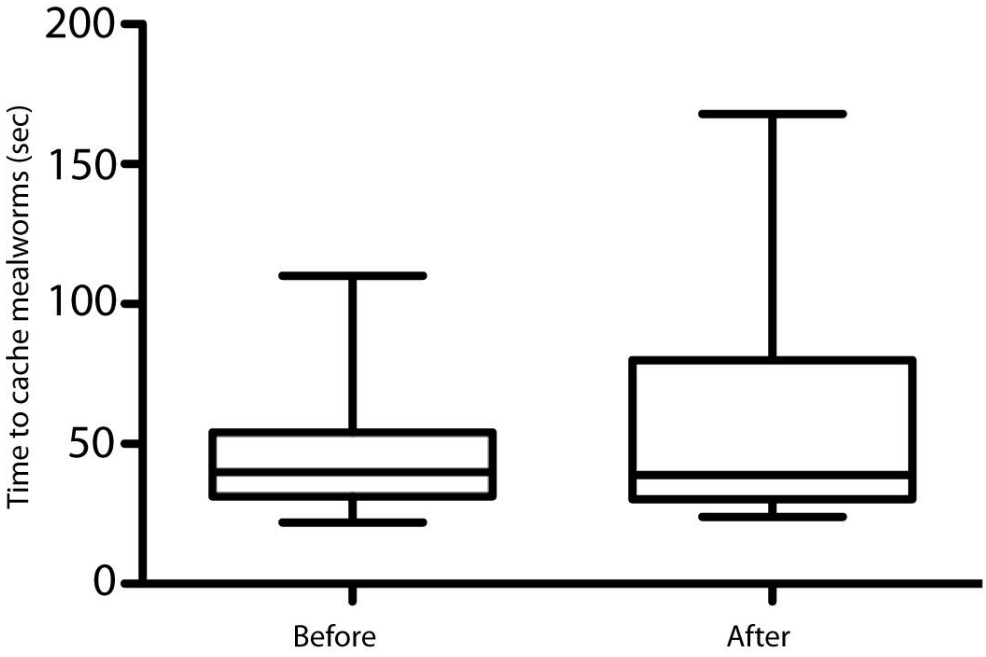

Figure 3.6. The time taken to cache mealworms before and after experimental cache pilfering. Shown are the medians, and 25th and 75th percentiles.

CHAPTER 4

Does the caching behaviour of the South Island robin (*Petroica australis australis*) change with observer presence?

4.1 Abstract. – Many studies of avian caching take place in an aviary/lab environment as most species show strong negative reactions to humans. Both the artificial environment and presence of humans may limit the applicability of such studies to wild populations of birds. Although these facts are well known, few studies have looked at how the presence of people alters an animal's behaviour. Here I examined how my presence may alter the caching behaviour of the South Island robin. I used two experiments on male robins. In the first experiment I tested whether robins altered their caching behaviour in response to changes in my attentional state. In the second experiment I tested whether robins changed their caching behaviour depending on how close I was standing to them while they were being fed. Robins have been shown to change the distance and height they placed caches after experimental pilfering (Chapter 3), so I expected both my attentional state and my distance to affect caching behaviour in ways that minimised cache theft. In other words, it would make sense for robins to benefit from knowing if another individual was watching them (and from how close it was watching them) because, from a pilferer's perspective, seeing a caching individual place a cache should improve its chances of finding the cache. However, in both sets of experiments robins did not change their caching behaviour except for caching more mealworms when I stood closer to the feeding point. No differences were found in time taken to cache, caching distance or caching height. These results suggest that robins either did not see me as a threat to their caches, or that they cannot distinguish between whether a person can see them or not.

4.2 **Introduction**

The most realistic studies of the behaviour of wild animals are those set in their natural environment (Rattenborg *et al.* 2008). However, wild animals often react directly to the presence of human observers because being watched and followed by a person is often perceived as a threat. Such reactions present problems for researchers trying to understand behaviour explicitly under 'natural' conditions. An important method for minimising the effects of an observer is to habituate the animals first. However, the applicability of data collected from habituated animals is often not questioned. Few researchers have addressed the issue, but they generally acknowledge that observer presence may change certain aspects of an animal's behaviour (e.g. Rasmussen 1991). Many of the effects are generally attributed to the impact of the human observer on the behaviour of other animals at the study site, such as predators, rather than to changes in the behaviour of the habituated individuals themselves (Rasmussen 1991). However, some contend that observer effects may be more widespread and significant on the focal individuals as well (Martin & Bateson 1986). As a result, conclusions drawn exclusively from studies of habituated animals should be treated with some caution (Crofoot *et al.* 2010).

Not all animals react to humans to the same extent. Animals on isolated islands evolved in the absence of many predators (including humans) and as a result are relatively tame even without periods of habituation. For example, New Zealand fantails (*Rhipidura fuliginosa*) and South Island robins (*Petroica a. australis*) are 'friendly' around humans and follow them as they move through the forest. These and other island birds appear to lack the predator avoidance and defence behaviours that their counterparts on continents have for protection against mammalian predators. Such tameness and naivety is likely to have been one reason for the high recent extinction rates of birds in New Zealand and

other Pacific Islands (King 1984; Towns & Daugherty 1994). The ability to recognise potential predators, including humans, likely has both genetic and learned components (Maloney & McLean 1995). For example, Maloney & McLean (1995) found that robins from a predator-free island population did not respond to the threat of a model stoat (*Mustela ermina*), whereas experienced robins from the mainland (sympatric with stoats) responded to the predator with more flights, wing-flicks and hops. They hypothesised that originally robins across New Zealand would have responded like an isolated island population before the introduction of mammalian predators and that predator recognition abilities of mainland birds have developed since the arrival of mammals (Maloney & McLean 1995).

Recognising predators and assessing the risk from different species of heterospecifics requires a certain degree of cognitive ability. Some birds and primates have been shown to display advanced cognitive abilities comparable to humans. However, there is often a discrepancy between the cognitive skills that these animals display in natural settings and those they display in controlled experimental or captive settings. One example is the ability of chimpanzees (*Pan troglodytes*) to understand what heterospecifics do and do not see when in captivity versus when in the wild. There may be a number of reasons for this inconsistent ability. One hypothesis is that interactions with humans in wild situations are unnatural, such as when a human is communicating to a chimpanzee about a food item. This situation is unusual for chimpanzees that compete almost exclusively with conspecific group mates to monopolise food resources (Hauser & Wrangham 1987). Thus, chimps may not understand the cooperative intentions of the human experimenter because it is so different to both the selective pressures their species has dealt with over its evolutionary history and with their own food-related experiences. However, a chimpanzee

raised in captivity may come accustomed to understanding human communications and cues.

Learning from conspecifics is one of the benefits of living in social groups. For example, individuals can potentially determine from the behaviour of others the location of food and/or predators. The gaze direction (i.e., head and eye direction) of other individuals is a pivotal source of information for humans but has also been demonstrated in a number of animals (Tomasello & Call 1997). Over the last 15 years, many studies have tested whether non-human animals have the ability to recognise another animal's gaze (Itakura 2004). It may be essential for the survival of some non-human animals to understand another individual's attention via the direction of their gaze; this is known as "looking where someone else is looking" (Corkum & Moore 1998). Gaze cues may be perceived and interpreted by animals in different ways. However, if gaze is used in a similar sense by animals as it is in humans, it is possible that animals can understand each other's context. Experiments have recently shown that a number of primates and other social mammals such as dogs, dolphins, and goats can follow gaze direction (Bugnyar *et al.* 2004). Itakura (1996) found that chimpanzees reliably followed experimenter pointing and head + eye cues. In a similar experiment, Povinelli & Eddy (1996) found that chimpanzees followed the experimenter's eye movements and not any other cues. Nevertheless, the degree and the context under which they can use gaze information varies from species to species (Call *et al.* 2000).

Interpreting information from the gaze of others has been proposed to be a crucial element of a "Theory of Mind" (TOM) (Baron-Cohen *et al.* 2001). TOM is the ability to use attentional mechanisms (i.e., gaze following, joint or shared attention), along with most likely higher-order cognitive strategies (such as experience of empathy) to represent,

interpret and predict the behaviour of others in terms of their mental state, such as their thoughts or goals (e.g. knowing, wanting, believing or seeing) about another individual or with respect to an object (Emery 2000; Goossens 2008; Heyes 1998). Individuals with such complex mental abilities could use them to predict and explain behaviour (Heyes 1998). Indeed, the capacity for non-human animals to attribute others with mental states has been the subject of considerable debate (Povinelli & Vonk 2003). TOM is thought to be pinnacle of animal cognition and there are an increasing number of primatologists and ornithologists that are questioning whether non-human animals have mental states. Many authors have suggested a TOM for non-human animals, but to date there has been no conclusive evidence despite much ongoing debate (Penn & Povinelli 2007). However, there is increasing evidence that TOM-like abilities may be present in species phylogenetically remote from humans, such as certain bird species (Emery & Clayton 2004; Dally *et al.* 2006). In general, researchers have distinguished between gaze following capacities that are based either on learned or simple reflexive responses and a more sophisticated appreciation, such as thinking about what others may be thinking about (e.g. Povinelli and Eddy 1996; Tomasello *et al.* 1999). In the latter case, gaze following may be an essential aspect of TOM.

Although the list of animals shown to use gaze is increasing, most species that respond to head orientation react little to more subtle indicators of attention and have difficulties using such cues in a cooperative context (Call *et al.* 1998, Call *et al.* 2000). Recently, some species have been found responsive to gaze direction in competitive situations (Hare *et al.* 2000, Von Bayern & Emery 2009). Von Bayern and Emery (2009) investigated the sensitivity of jackdaws (*Coloeus monedula*) to subtle attentional and communicative cues. Jackdaws are social corvids that form pair bonds and exhibit

analogous eye morphology to humans, in the sense that they have a dark pupil surrounded by a white of the eye. When they were placed into a conflict scenario in which food was presented in front of a human, the jackdaws took more time to retrieve the food when the person was looking at the food than if they were looking away from it. This was only the case when the person was unfamiliar; when the birds spent long periods of time with a person they learnt were non-threatening they were not as cautious (Von Bayern and Emery 2009). Bugnyar & Kotrschal (2002) suggested that the capacity for observational spatial memory in corvids represented the catalyst for an 'evolutionary arms race' between cachers and pilferers, such that pilferers should develop methods for observing cachers as unobtrusively as possible, and cachers develop strategies to counter the risk of cache pilferage (Clayton *et al*. 2007).

Like corvids, South Island robins cache some of their prey for later consumption, but these caches are sometimes pilfered by both conspecifics and heterospecifics (Steer 2006). Locating hidden caches is probably difficult for potential pilferers unless they are able to follow the caching bird as it creates its cache (i.e., gazing at the caching birds). From a caching robin's perspective, however, being watched by another individual could increase the risk its cache is later pilfered. Thus, one might expect a "watched" robin to alter its caching behaviour in such a way as to reduce cache pilfering, such as caching further away or in places out of an observer's gaze. By feeding mealworms to South Island robins while expressing different attentional states, I experimentally tested whether robins would alter their caching behaviour in response to my attentional state and to the distance I stood from the feeding point. My predictions are based on the assumptions that robins would find me less of a threat when being fed mealworms if my gaze was directed elsewhere and if I was further away from the food. Specifically related to attentional state,

I tested the following predictions: (1) robins will cache more prey when I was looking away from them; (2) robins will cache further away when looking at them; (3) robins will cache higher up when looking at them; and (4) robins will spend less time in the feeding circle when looking at them. Specifically related to distance, I tested the following predictions: (1) robins will cache more prey when I was standing further away; (2) robins will cache further away when I was standing close; (3) robins will cache higher up when I was standing close; and (4) robins will spend less time in the feeding circle when I was standing close.

4.3 Methods

Study site and species

For a complete description of the field sites and study species refer to Chapter 2.

Field experiment

To determine if caching behaviour varies with observer presence, I offered mealworms to robins and measured their caching patterns. I tested two hypotheses: (1) do robins change their caching behaviour based on their response to three different attentional states of the observer while being fed mealworms; and (2) do robins change their caching behaviour based on their response to how close a human observer stands while feeding them mealworms? Robins readily approach humans to within 1-5 m in a natural setting and cache mealworms offered to them within their territories. All birds (n = 11 birds) were identified by permanent leg bands and sexes were confirmed with banding records. In the summer of 2009/2010 almost all the robins were banded at both field sites. Trials were conducted between 9 am and 4 pm (NZST) and were halted if interrupted by strong winds

or moderate to heavy rainfall. Juveniles, whose sex is difficult to identify, were excluded from trials.

In the first set of experiments, I positioned myself into one of three different attentional states when feeding robins: (1) looking forward, (2) looking to the side and (3) looking behind. In each case, my gaze was relative to that of the robin. Thus, in "looking forward," my gaze was directed towards the robin and my eyes followed it wherever it moved. "Looking to the side" involved maintaining my gaze at approximately 90 degrees from the robin, while when "looking behind" my gaze was directly opposite the bird (180 degrees). This allowed me to potentially alter the bird's perception of pilfering of a cache and/or risk of predation by the observer, under the assumption that an observer directly staring at the robin would pose a greater risk than an observer with its gaze directed ever increasingly away from the bird. I assigned each state a number and used a random number generator to decide the order in which I tested each of the 3 attentional states prior to starting each experiment. I was able to tell when a robin had flown away from the feeding circle and in what direction because I filmed the feeding point with a Sony Handycam and I could watch the robin on the screen. After the robin had flown away I had to turn around so I could see where it placed its cache. Therefore, the attentional state is not absolute because I had to spend sometime staring at the bird. In the second set of experiments, I tested the effect of observer distance on caching behaviour of robins by altering the distance between myself and the focal bird while providing them with mealworms. I stood at three different distances (1 m, 2 m and 3 m) from a fixed feeding point while feeding robins. From each distance, I then threw in mealworms one at a time. The order in which I stood at different distances was randomly assigned prior to each experiment. At each distance, I used the same attentional state of "looking forward".

To begin each experiment, robins were first located by sight or by their song. To attract robins to within a few metres, I used either clapping, singing, and pishing sounds, or by hitting broken branches against trees. In all cases, these noises attracted robins to my immediate vicinity. I also cleared a circular area of ground about 75 cm diameter of all dead leaves and ferns to use as the feeding point. Robins were readily attracted to the disturbed ground, perhaps to feed on the invertebrates uncovered. The experiments were only started when the males were accompanied by their partner in the nearby vicinity (within 10 m). When the male robin was within 4 m, I began the trial by throwing a mealworm into the centre of the feeding point. Prior to the experiments, I weighed each mealworm (to 0.001 g) on a Ohaus Scout Pro Portable scale. Mealworms used in the experiment weighed between 0.090 and 0.150 g. The size of mealworms fed was relatively large because large mealworms are more likely to be cached than small mealworms (Chapter 2) and I wanted to limit variation in response to my experiments that might be due to prey size. The next mealworm was fed to the robin once the previous one had been eaten or the robin had returned after caching.

I conducted trials only on male robins, however, at the start of experiments they were always accompanied by their mates. Only males were tested because females are subordinate and cache few mealworms because they are chased away by males (Burns 2009). Sometimes a rival (or neighbouring) male showed up at the trial; this interaction would usually result in one male chasing the other off. If the male did not return after 5 minutes then the trial was started again the following day. Most birds consumed 5 to 10 mealworms before starting to cache additional mealworms in nearby trees. Enough mealworms were fed to each robin so that they cached at least 10 items. A mealworm was defined as cached if it was transported in a robin's bill and deposited in a new location. All

mealworms offered to birds were either consumed or cached. Male robins consistently acquired the mealworms I threw out during trials; females either stood by but did not attempt to eat mealworms or they were chased away by their partner. However, females did acquire mealworms later from their partner's caches by pilfering (personal observation). Cached mealworms were first immobilised by being crushed between the bird's mandibles or pecked.

Statistical analysis

I quantified three dependent variables to characterize the reaction of male robins to my presence. First, I recorded the time from when the robin entered the feeding point to when it left the feeding point. This is referred to as time spent at feeding point. I then measured both the height and the horizontal distance of each cache from the food source. This was done after the trial was complete to avoid disturbing caches and thereby potentially changing the subsequent caching behaviour of the birds. To remember locations of caches during the trial, I noted the direction, approximate height and distance, tree species, and any defining characteristics of the cache in a notebook. In all cases, I was successful in relocating caches after the trial was complete. Both horizontal distance and height were measured with a measuring tape. Horizontal distance was measured as the distance between the experimental food source (i.e., the location on the forest floor where the mealworms were placed) and the point on the ground below the cache site. Height was measured as the distance between the cache site and the point directly below on the forest floor. I used Friedman tests to determine if the variables cached/not cached, distance from the feeding point, height of cache and time spent at the feeding point were affected by my attentional state and distance from the feeding point. Friedman tests were used because

treatments were not independent because within each treatment I compared the same 11 individuals. Dunn's multiple comparison tests were used to compare the medians of one size class to another size class.

4.4 Results

Attentional state had no affect on whether mealworms were cached or not (Figure 4.1; Q = 1.48, p = 0.47). For mealworms that were cached, there was no significant difference between my attentional state and the horizontal distance to cache (Figure 4.2; Q= 0.40, p = 0.82), height of cache (Figure 4.3; Q= 1.31, p = 0.52) or the time the robin took between grabbing the mealworm and leaving the feeding circle (Figure 4.4; Q= 1.39, p = 0.50).

The distance I stood from the feeding circle significantly affected whether mealworms were cached or not (Figure 4.5; Q = 6.55, p = 0.04). The Dunn's multiple comparison tests showed there was a difference between 2 and 3 m but no difference between 1 and 3 m, nor between 1 and 2 m. Robins appeared to be more likely to cache at the greatest distance (3 m), although it should be noted the differences between the 3 distances were not large. For mealworms that were cached, there was no significant difference between my attentional state and the horizontal distance to cache (Figure 4.6; Q = 4.23, p = 0.12), height of cache (Figure 4.7; Q = 1.76, p = 0.40) or the time the robin took between grabbing the mealworm and leaving the feeding circle (Figure 4.8; Q = 2.36, p = 0.35).

4.5 Discussion

Placed into a situation in which preferred food was presented in front of a human in different scenarios, wild robins did not change any aspect of their caching behaviour depending on the observer's attentional state but changed one aspect depending on the distance I stood from the feeding circle. The only significant difference occurred when I stood between 2 or 3 metres from the bird. I expected robins to change their caching behaviour when the perceived risk of having caches pilfered was at its lowest, such as when I had my back turned and was looking in the opposite direction to the robin, and when I was standing furthest (3 m) from the feeding circle. I predicted the robins would cache closer to the feeding point, at a lower height, spend more time in the feeding circle and cache more mealworms because these two variables were also expected to be the least threatening. Instead, the robin's behaviour did not change in response to my attentional state. However the robins cached more mealworms when I stood further away from the feeding circle. This was only the case when comparing 2 and 3 m, for an unknown reason there was lots of variability when I stood 1 m away. Although most of the results did not support my predictions, the results are not surprising given the 'friendly' nature of robins. In other words, like most New Zealand birds, robins appear to lack many of the antipredator behaviours commonly found in continental birds. For example, native New Zealand birds take longer to flush off the nest by an approaching human, whereas exotic species living in New Zealand flush much earlier (Burford 2011). It is possible that the robins in my experiments did not alter their behaviour as in none of the situations I created did the birds perceive me to be a threat, either to their caches or to their safety.

It is possible that the robins, despite being "tame" and free-living, still habituated to my presence because I was a familiar presence in their territories. For example, when I first started exploring the bush for robins they were more timid and a few birds were so

timid that I had to exclude them from the study because they wouldn't come to food regularly. To band birds at my field sites sometimes took several days of feeding with mealworms before they would come close enough to me to catch. Nevertheless, even though I had captured and put robins through a potentially stressful ordeal, this did not appear to make them more fearful of me. Instead, robins often re-appeared within minutes of release, sitting on a nearby branch or the ground, seemingly waiting to be fed mealworms. It is because of this level of acceptance around me, and increasing level of habituation, that they may have not responded differently to my attentional state or variation in the distance away I stood.

A month prior to the experiments reported in this chapter, I had experimentally pilfered the caches of the robins to determine if their subsequent caching behaviour changed after perceiving me as a pilferer (refer to Chapter 3). In that study, I found robins did change their caching behaviour after experiencing experimental pilferage. My conclusion was that the robins responded to me as a threat to their caches. Thus, it is possible that recognising me as a threat had not been maintained to the time of the current study. Given that robins were not pilfered by humans in the time period between the first experiment and the present set of experiments, it is likely they simply no longer considered me a threat. It would be interesting to redo the experiments described in this chapter immediately after pilfering caches in order to see if attentional states can affect caching behaviour when the experience is more recent. In other words, it is possible that robins can use attentional states, but had no reason to do so simply because their caches had not been pilfered by me recently, and thus they did not consider me enough of a threat to warrant any change in their caching behaviour.

Caching is a competitive behaviour that requires animals to cache in ways that reduce the amount of pilferage. Being able to judge what direction a conspecific is looking should help an individual avoid others seeing where its caches are placed. It remains possible that subtle behavioural changes occurred in caching behaviour that I was not able to distinguish using the relatively crude measure of activity used in my experiments. While observer presence did not affect any of my variables, the robins may have carried out different types of activities when I was unaware. For example, robins may have spent more time being vigilant and less time resting or preening when I was present. Although further data is needed to test this idea, it is clear that large scale changes in caching behaviour were not evident due to my presence or my attentional state.

Common ravens (*Corvus corax*) are known to follow a conspecific's visual gaze into space and behind visual barriers (Bugnyar *et al.* 2004). Such gaze following skills should have pronounced benefits in socio-ecological settings. For ravens and other caching animals, having the ability to follow the direction of an individual's gaze may be advantageous for protecting their caches from pilfering, i.e. caching out of sight (Schloegl *et al.* 2007). Likewise, knowing an animal is not watching when their back is turned would obviously be beneficial as well. Since robins changed their caching behaviour the day after I had pilfered their caches (Chapter 3), it is possible they specifically recognised me. Recognising other individuals would be particularly beneficial for robins because they regularly pilfer caches made by their partner; this behaviour is likely to be more evolutionally stable than if they were losing caches to unrelated competitors (which also occurs). Therefore, recognising other individuals for robins is important and makes them prime candidates for being capable of using the gaze of others in caching experiments that provides a conflict scenario (Schloegl *et al.* 2008).

My results are similar to those found in a study by von Bayern & Emery (2009) that looked at the response of jackdaws to human attentional states. They found that jackdaws did not take longer to retrieve food when they were placed in a situation in which food was placed in front of a human, no matter what the person's attentional state. However, when the person had had no prior contact with the jackdaws they took longer to retrieve food, especially when the person was directing their eyes at the reward as opposed to when they were looking away from it. A study on starlings (*Sturnus vulgaris*) found similar results: starlings approached food faster when a predator was looking away rather than directly at the food (Carter *et al.* 2008), whereas in similar study, house sparrows (*Passer domesticus*) showed no sensitivity to eye-gaze direction (Hampton & Sherry 1994). These results could mean that jackdaws and starlings understand the role of the eyes in perception, but a more conservative explanation is their response is the result of a low-level cognitive mechanism, i.e., sensitivity to eye orientation (von Bayern & Emery 2009). Prey animals might be expected to be sensitive to eye orientation because of the benefit of being able to assess predation risk and likewise for predators assessing if prey are being vigilant. It may have also evolved because of intraspecific selection pressures, such as cooperation with a partner or group mates and competition between conspecifics. von Bayern & Emery (2009) suggest that due to the similar appearance of human eye and that of a jackdaw, this makes it easy to follow the direction of their gaze and may help them to detect human eye gaze. Also behaviourally, there are several indications that jackdaws employ eye signals to communicate with conspecifics, most importantly their long-term partner (von Bayern & Emery 2009). In contrast, robins have all black eyes and this could make following a conspecifics gaze much more difficult. Therefore, robins may not be physically able to follow the gaze of other robins (apart from direction of head

movements) and because of their natural history not developed the ability to process gaze signals.

Daly *et al.* (2004) suggest western scrub-jays (*Aphelocoma californica*) may be aware of a conspecific's visual perception, because it appears they choose cache sites based on the social context and their surroundings. Cache site choice may stem from the potential threat posed by the observer because birds in the presence of conspecifics were more likely to cache in a shaded tray which means potential pilferers can learn less information about the cache site, and the chance of theft is reduced (Daly *et al.* 2004). It is possible that the scrub-jays understand what another bird can and cannot see, but a more conservative theory is that the scrub-jays are only aware of what they can see; for example, when they cache in locations that other birds cannot see, it may appear to them that the observers are absent ('out-of-sight, out-of-mind') (Daly *et al.* 2004).

Many animals use well-developed senses of sound, smell and sight to recognise conspecifics. While it is important to recognise conspecifics, such as your partner, offspring, etc., the importance of knowing individuals of a different species is not clear. Domestic animals are well known to recognise people, some nondomestic animals appear to recognise human features and specific people that they can associate with specific past experiences (Davis 2002; Levey *et al.* 2009). Marzluff *et al.* (2010) demonstrated American crows (*Corvus brachyrhynchos*) were able to recognise the facial features of people for a long period if they had a brief negative interaction with that person in the past. Crows would only mob dangerous people with a known history of trapping crows. Their experiments showed facial features were important indicators of recognition and not other features of the human body, such as movement and clothing (Marzluff *et al.* 2010). These learned responses may be related to the development of the hippocampus, a part of the

brain also well developed in caching birds. The hippocampus helps with learning the spatial and temporal context of the cues associated with danger (Olsson & Phelps 2007). Thus, caching birds like New Zealand robins make ideal specimens for the studying gaze because they quite likely have an enlarged hippocampus to cope with the spatial memory required to cache food but their enlarged hippocampus may predispose them to understand the gaze cues of other animals.

Hare *et al*. (2001) proposed the competitive cognition hypothesis with respect to chimpanzee cognition and why there was an inconsistent pattern of results for using gaze cues and their reason could equally apply to birds. Their hypothesis predicts animals will demonstrate the most motivation in competitive, rather than in cooperative experiments because unlike humans who communicate altruistically to others (e.g. the location of a monopolisable food resource), altruism and cooperation is not something chimpanzees have evolved (see also Tomasello *et al.* 2003). However, not all experiments showed a change in behaviour when placed in different competitive scenarios, therefore, learning rather than motivation may have a part to play in their results; subjects may have benefited in later experiments from learning in previous experiments (Hare & Tomasello 2004). Cognitive skills are thought evolve to solve ecological problems relevant to maximising survival and reproduction, and so to understand the process of cognitive evolution in any species we must identify the types of ecological problems that have driven their cognitive evolution. We must also attempt to understand how cognitive skills are integrated with and possibly constrained by other psychological systems (e.g. emotional/motivational) that have also evolved to maximise survival and reproduction (Hare & Tomasello 2004).

There may be a number of reasons for the lack of response of robins to my presence and attentional state. One idea is that these experiments are too unnatural. The

situation is clearly unusual for the robins which are use to competing with their own species and other forest animals for monopolisable food resources. Thus, robins may not understand the competitive motive of the human communicator in these experiments because it is dissonant with both the selective pressures their species has faced during its evolutionary history and with their own previous food-related experience. Robins may not recognise certain kinds of intentional or mental states, and they may have trouble in developing strategies in situations in which they must use their knowledge to imagine what another might see in some totally novel situation. Caching produces a complex social environment and robins must constantly find new ways to compete against their conspecifics if they want to make the most of the resources available to them, or else they will not be in good condition or survive long enough to pass on their own genes. It seems logical that robins may have evolved social-cognitive abilities to allow individuals to outcompete competitors, and so it is scenarios like these that we are most likely to see animals with these abilities. It is for this reason and because how easy it is to study robins in the wild that make them ideal species to study avian cognition.

4.6 Literature cited

Baron-Cohen, S., Wheelwright, S., Hill, J., Raste, Y. & Plumb, I. 2001. The "reading the mind in the eyes" test revised version: a study with normal adults, and adults with asperger syndrome or high-functioning autism. *The Journal of Child Psychology and Psychiatry and Allied Disciplines*, **42**, 241-251.

Bugnyar, T. & Kotrschal, K. 2002. Observational learning and the raiding of food caches in ravens, *Corvus corax*: is it `tactical' deception? *Animal Behaviour*, **64**, 185-195.

Bugnyar, T., Stöwe, M. & Heinrich, B. 2004. Ravens, *Corvus corax*, follow gaze direction of humans around obstacles. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, **271**, 1331-1336.

Burford, M. D. 2011. A comparative analysis of nesting life-history traits and the risk of predation among island and continental birds. Unpublished MSc thesis, University of Canterbury, Christchurch, New Zealand.

Burns, K. 2009. Fine-scale food hoarding decisions in New Zealand robins (*Petroica australis*): is inter-sexual competition important? *Journal of Ornithology*, **150**, 321-328.

Call, J., Agnetta, B. & Tomasello, M. 2000. Cues that chimpanzees do and do not use to find hidden objects. *Animal Cognition*, **3**, 23-34.

Call, J., Hare, B. A. & Tomasello, M. 1998. Chimpanzee gaze following in an object-choice task. *Animal Cognition*, **1**, 89-99.

Carter, J., Lyons, N. J., Cole, H. L. & Goldsmith, A. R. 2008. Subtle cues of predation risk: starlings respond to a predator's direction of eye-gaze. *Proceedings of the Royal Society B: Biological Sciences*, **275**, 1709-1715.

Clayton, N. S., Dally, J. M. & Emery, N. J. 2007. Social cognition by food-caching corvids. The western scrub-jay as a natural psychologist. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **362**, 507-522.

Corkum, V. & Moore, C. 1998. The origins of joint visual attention in infants. *Developmental Psychology*, **34**, 28-38.

Crofoot, M. C., Lambert, T. D., Kays, R. & Wikelski, M. C. 2010. Does watching a monkey change its behaviour? Quantifying observer effects in habituated wild primates using automated radiotelemetry. *Animal Behaviour*, **80**, 475-480.

Davis, H. 2002 Prediction and preparation: Pavlovian implications of research animals discriminating among humans. *Institute for Laboratory Animal Research Journal*, **43**, 19-26.

Dally, J. M., Clayton, N. S. & Emery, N. J. 2006. The behaviour and evolution of cache protection and pilferage. *Animal Behaviour*, **72**, 13-23.

Dally, J. M., Emery, N. J. & Clayton, N. S. 2004. Cache protection strategies by western scrub-jays (*Aphelocoma californica*): hiding food in the shade. *Proceedings: Biological Sciences*, **271**, S387-S390.

Emery, N. J. 2000. The eyes have it: the neuroethology, function and evolution of social gaze. *Neuroscience & Biobehavioral Reviews*, **24**, 581-604.

Emery, N., Dally, J. & Clayton, N. 2004. Western scrub-jays (*Aphelocoma californica*) use cognitive strategies to protect their caches from thieving conspecifics. *Animal Cognition*, **7**, 37-43.

Goossens, B. M. A., Dekleva, M., Reader, S. M., Sterck, E. H. M. & Bolhuis, J. J. 2008. Gaze following in monkeys is modulated by observed facial expressions. *Animal Behaviour*, **75**, 1673-1681.

Hampton, R. R. & Sherry, D. F. 1994. The effects of cache loss on choice of cache sites in black-capped chickadees. *Behavioral Ecology*, **5**, 44-50.

Hare, B., Call, J., Agnetta, B. & Tomasello, M. 2000. Chimpanzees know what conspecifics do and do not see. *Animal Behaviour*, **59**, 771-785.

Hare, B., Call, J. & Tomasello, M. 2001. Do chimpanzees know what conspecifics know? *Animal Behaviour*, **61**, 139-151.

Hare, B. & Tomasello, M. 2004. Chimpanzees are more skilful in competitive than in cooperative cognitive tasks. *Animal Behaviour*, **68**, 571-581.

Hauser, M, D. & Wrangham, R. W. 1988. Manipulation of food calls in captive chimpanzees (a preliminary report). *Folia primatologica*, **48**, 207-210.

Heyes, C. M. 1998. Theory of mind in nonhuman primates. *Behavioral and Brain Sciences*, **21**, 101-114.

Itakura, S. 1996. An exploratory study of gaze-monitoring in nonhuman primates1. *Japanese Psychological Research*, **38**, 174-180.

Itakura, S. 2004. Gaze-following and joint visual attention in nonhuman animals. *Japanese Psychological Research*, **46**, 216-226.

King, C. B. 1984. Immigrant killers. Introduced predators and conservation of birds in New Zealand. Oxford University Press, Auckland, New Zealand.

Levey, D. J., Londoño, G. A., Ungvari-Martin, J., Hiersoux, M. R., Jankowski, J. E., Poulsen, J. R., Stracey, C. M. & Robinson, S. K. 2009. Urban mockingbirds

quickly learn to identify individual humans. *Proceedings of the National Academy of Sciences*, **106**, 8959-8962.

Maloney, R. F. & McLean, I. G. 1995. Historical and experimental learned predator recognition in free-living New Zealand robins. *Animal Behaviour*, **50**, 1193-1201.

Martin, P. & Bateson, P. 1986. Measuring behaviour: an introductory guide. Cambridge University Press, Cambridge, England. Cited in **Lehner, P. N.** 1987. Design and execution of animal behavior research: an overview. *Journal of Animal Science*, **65**, 1213-1219.

Marzluff, J. M., Walls, J., Cornell, H. N., Withey, J. C. & Craig, D. P. 2010. Lasting recognition of threatening people by wild American crows. *Animal Behaviour*, **79**, 699-707.

McLean, I. G., Hölzer, C. & Studholme, B. J. S. 1999. Teaching predator-recognition to a naive bird: implications for management. *Biological Conservation*, **87**, 123-130.

Olsson, A. & Phelps, E. A. 2007. Social learning of fear. *Nature Neuroscience*, **10**, 1095-1102.

Penn, D. C. & Povinelli, D. J. 2007. On the lack of evidence that non-human animals possess anything remotely resembling a 'theory of mind'. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **362**, 731-744.

Povinelli, D. J. & Eddy, T. J. 1996. Chimpanzees: joint visual attention. *Psychological Science*, **7**, 129-135.

Povinelli, D. J. & Vonk, J. 2003. Chimpanzee minds: suspiciously human? *Trends in Cognitive Sciences*, **7**, 157-160.

Rasmussen, D. R. 1991. Observer influence on range use of *Macaca arctoides* after 14 years of observation? *Lab Primate News*, **30**, 6-11. Cited in **Williamson, E. A. & Feistner, A. T. C.** 2003. Habituating primates: processes, techniques, variables and ethics. In: **Setchell, J. M. & Curtis, D. J.,** (editors). Field and laboratory methods in primatology: a practical guide. Cambridge University Press, Cambridge, England.

Rattenborg, N. C., Voirin, B., Vyssotski, A. L., Kays, R. W., Spoelstra, K., Kuemmeth, F., Heidrich, W. & Wikelski, M. 2008. Sleeping outside the box: electroencephalographic measures of sleep in sloths inhabiting a rainforest. *Biology Letters*, **4**, 402-405.

Schloegl, C., Kotrschal, K. & Bugnyar, T. 2007. Gaze following in common ravens, *Corvus corax*: ontogeny and habituation. *Animal Behaviour*, **74**, 769-778.

Schloegl, C., Kotrschal, K. & Bugnyar, T. 2008. Do common ravens (*Corvus corax*) rely on human or conspecific gaze cues to detect hidden food? *Animal Cognition*, **11**, 231-241.

Steer, J. 2006. Seasonality of food use and caching in New Zealand robins (*Petroica australis*). MSc thesis, Victoria, University of Wellington.

Tomasello, M. & Call, J. 1997. Primate Cognition. Oxford University Press, Oxford, England.

Tomasello, M., Call, J. & Hare, B. 1998. Five primate species follow the visual gaze of conspecifics. *Animal Behaviour*, **55**, 1063-1069.

Tomasello, M., Call, J. & Hare, B. 2003. Chimpanzees understand psychological states – the question is which ones and to what extent. *Trends in Cognitive Sciences*, **7**, 153-156.

Tomasello, M., Hare, B. & Agnetta, B. 1999. Chimpanzees, *Pan troglodytes*, follow gaze direction geometrically. *Animal Behaviour*, **58**, 769-777.

Towns, D. R. & Daugherty, C. H. 1994. Patterns of range contractions and extinctions in the New Zealand herpetofauna following human colonisation. *New Zealand Journal of Zoology*, **21**, 325-339.

von Bayern, A. M. P. & Emery, N. J. 2009. Jackdaws respond to human attentional states and communicative cues in different contexts. *Current Biology*, **19**, 602-606.

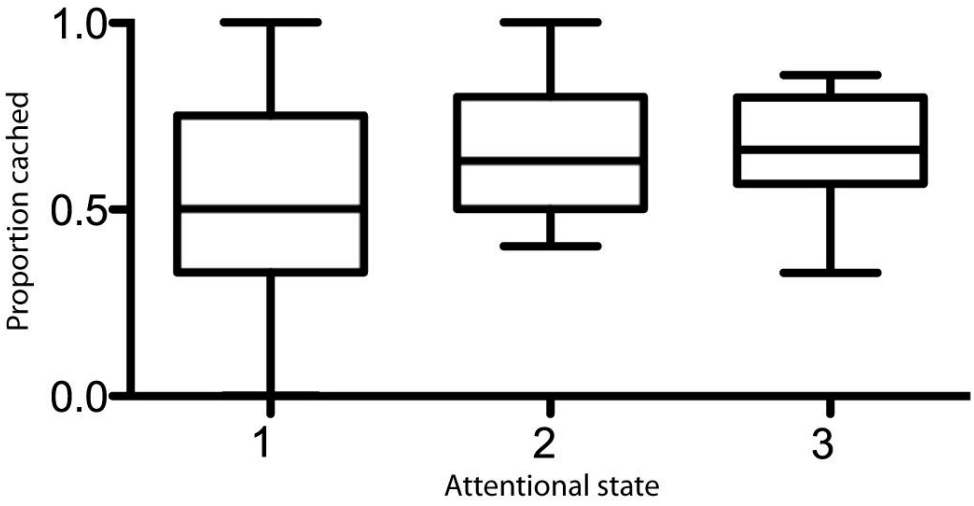

Figure 4.1. The proportion of mealworms cached depending on the attentional state of the human observer: (1) looking forward, (2) looking to the side and (3) looking behind.

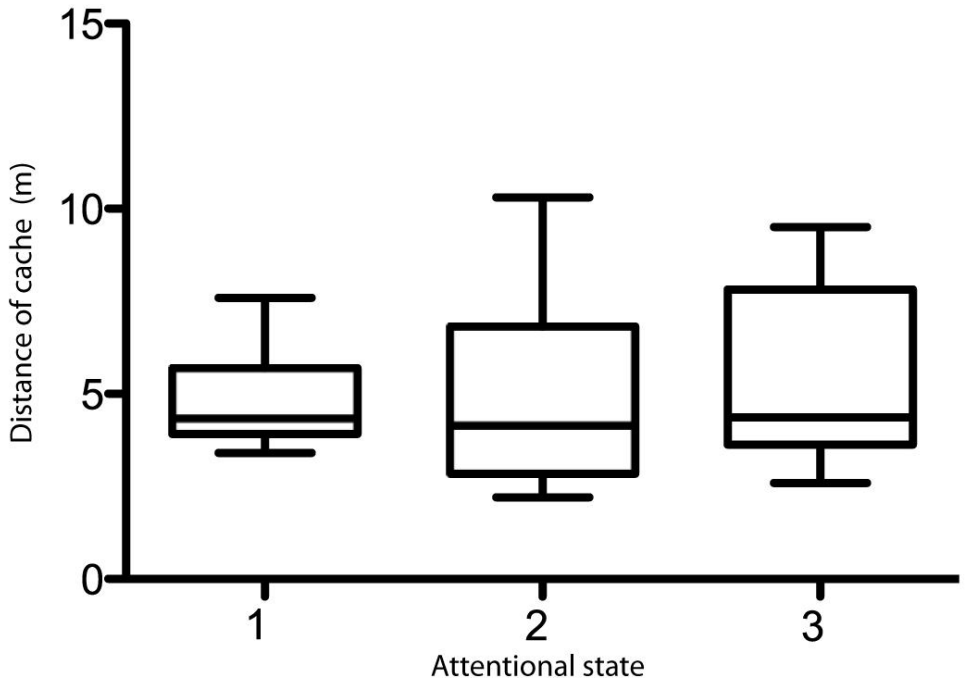

Figure 4.2. The distance of the caches from the feeding circle depending on the attentional state of the human observer: (1) looking forward, (2) looking to the side and (3) looking behind.

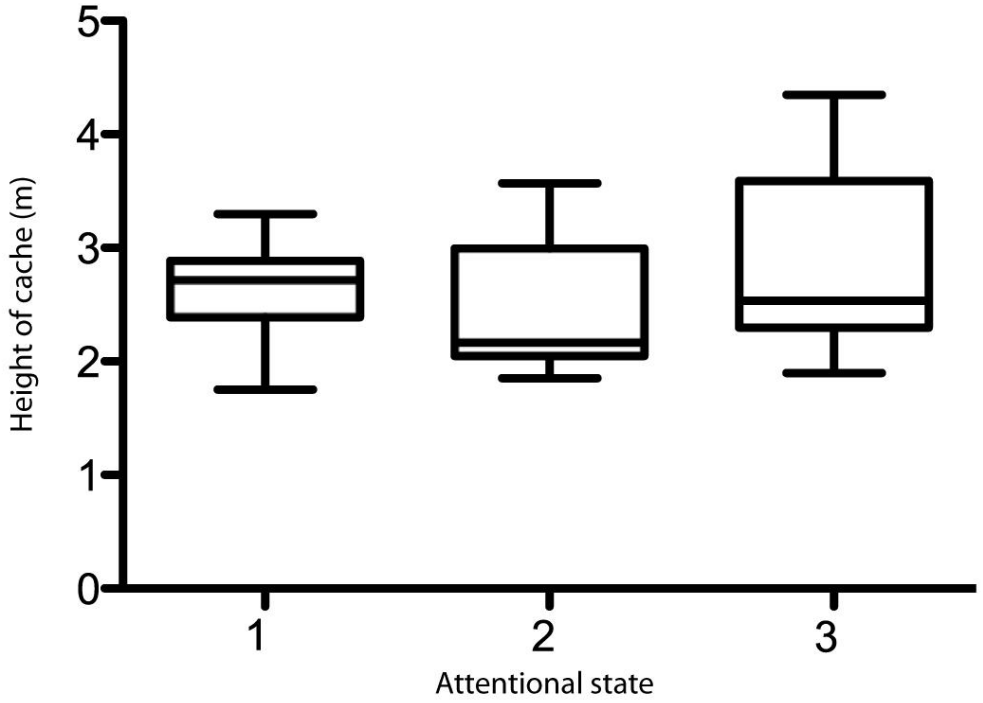

Figure 4.3. The height of the caches off the ground depending on the attentional state of the human observer: (1) looking forward, (2) looking to the side and (3) looking behind.

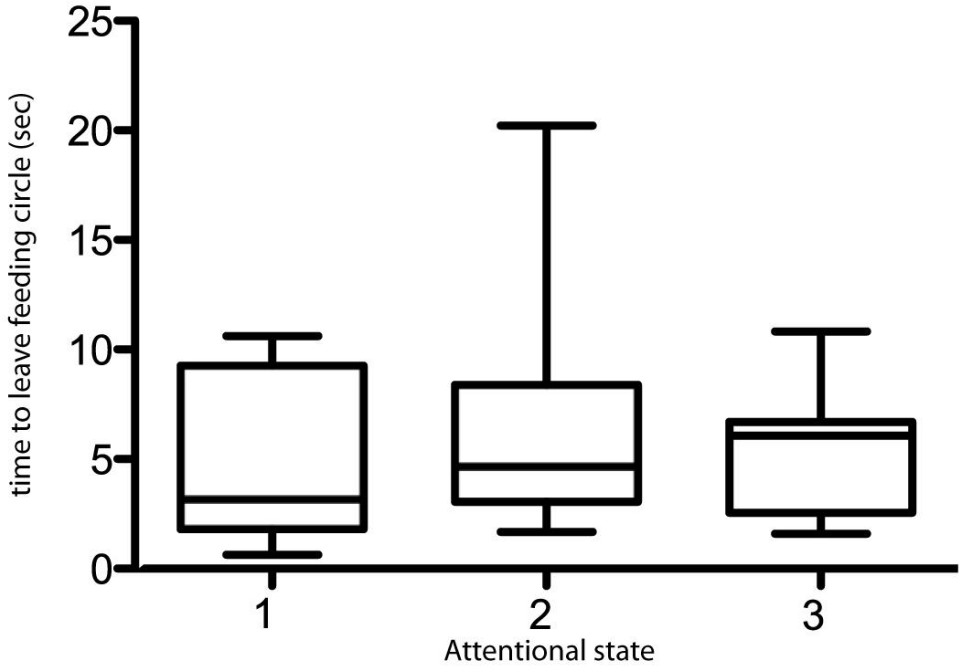

Figure 4.4. The time taken to pick up the mealworm and leave the feeding circle depending on the attentional state of the human observer: (1) looking forward, (2) looking to the side and (3) looking behind.

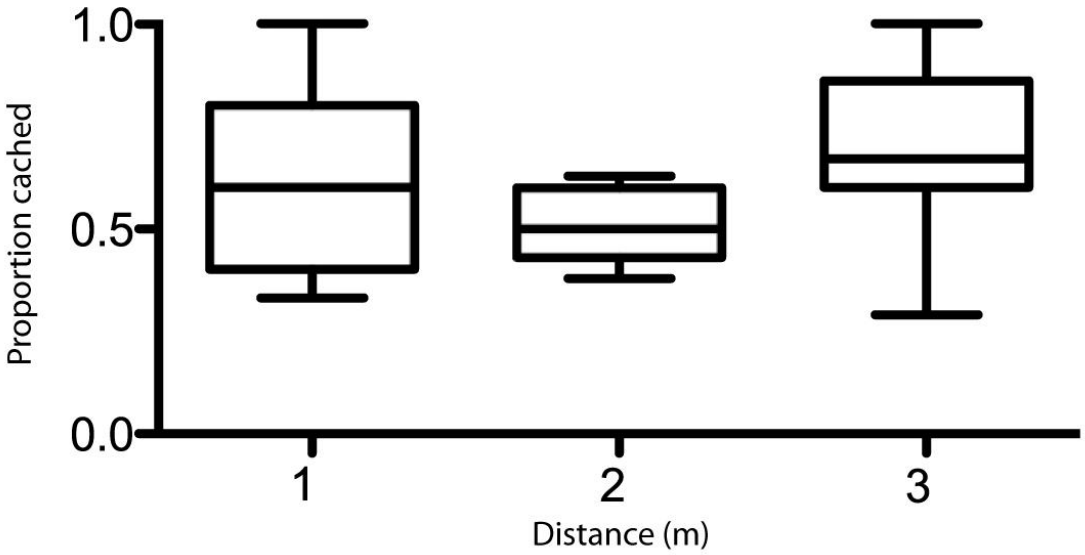

Figure 4.5. The proportion of mealworms cached depending on the distance from the feeding point the human observer was standing.

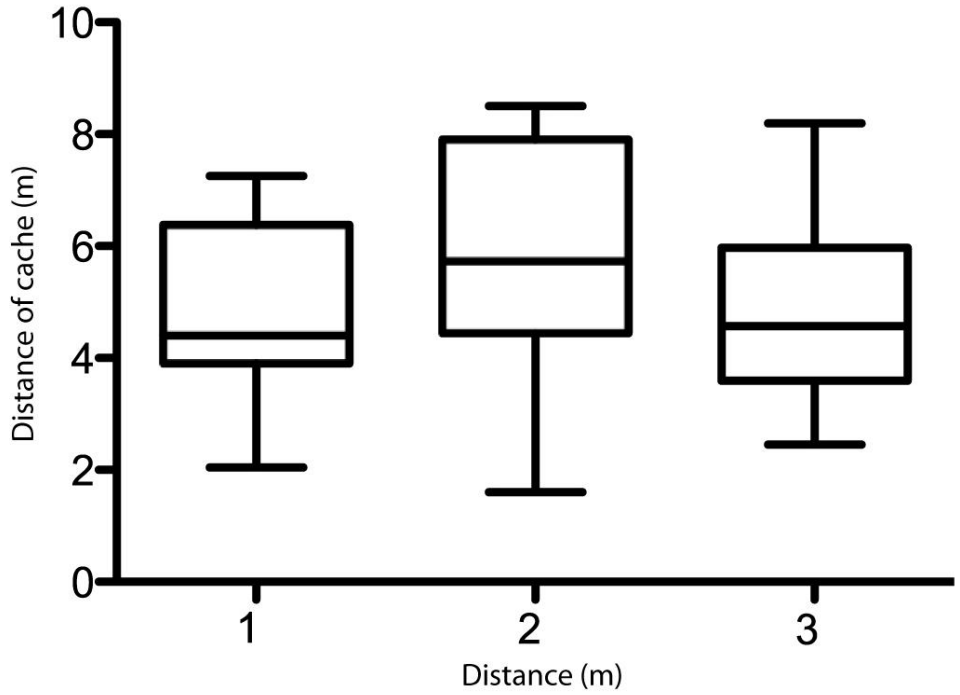

Figure 4.6. The length of the caches from the feeding circle depending on the distance from the feeding point the human observer was standing.

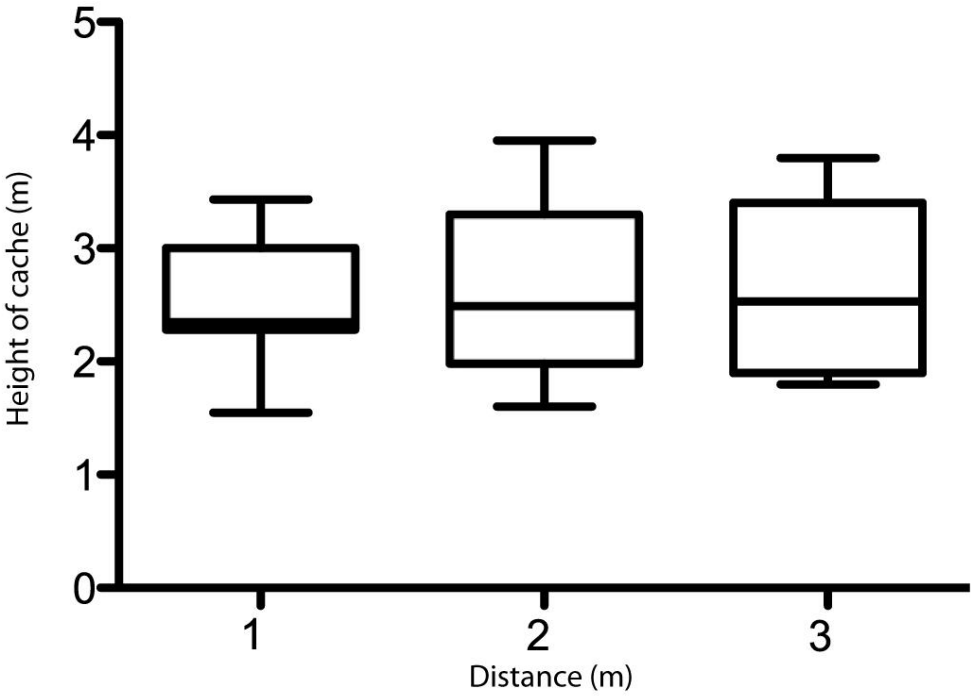

Figure 4.7. The height of the caches off the ground depending on the distance from the feeding point the human observer was standing.

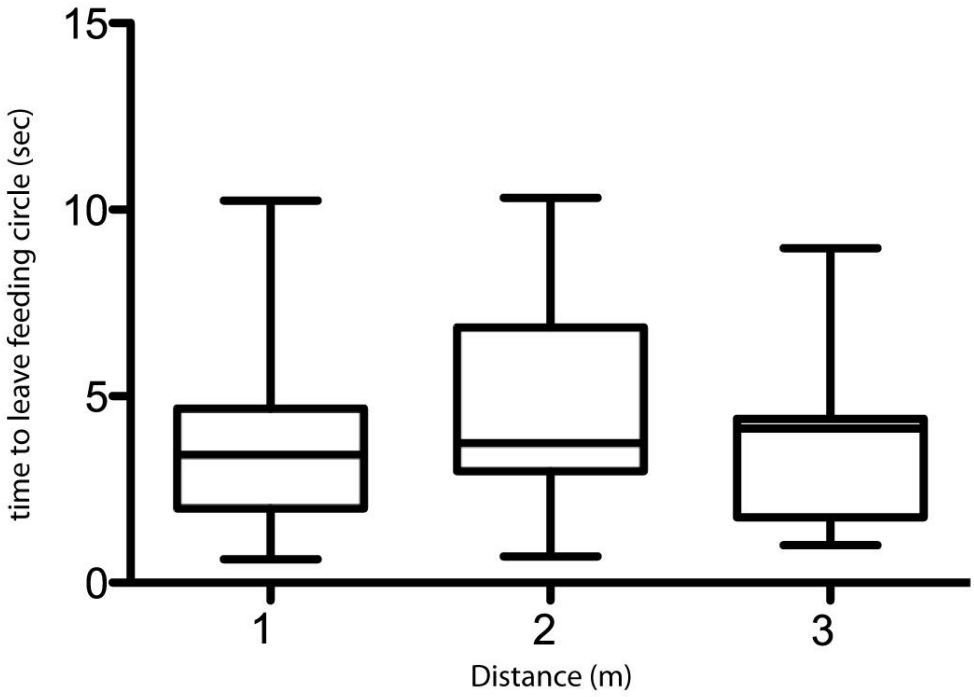

Figure 4.8. The time taken to pick up the mealworm and leave the feeding circle depending on the distance from the feeding point the human observer was standing.

CHAPTER 5

Summary, conclusions and suggestions for future research

5.1 Summary

Caching likely evolved in birds that are regularly faced with an excess of food, but in which the nature of the food type means it can be shifted for future consumption (see Roberts 1979). The vast majority of research on caching behaviour of birds has revolved around Northern Hemisphere species, especially the families Corvidae (crows and jays) and Paridae (chickadees and titmice). Earlier work, in particular, was aimed at understanding the spatial distribution of caches (e.g., Cowie *et al.* 1981; James & Verbeek 1985; Sherry *et al.* 1982). However, more recent work has focussed on the underlying behaviours that collectively allow birds to make successful choices of when, what, and where to cache as well as how to alter caching behaviour when others may be witnesses (Clayton *et al.* 2007; Dally *et al.* 2004; Dally *et al.* 2005a; Dally *et al.* 2006). These experiments have generally occurred in the controlled confines of a lab, mostly because of the difficulties of following birds and their caches in the field. Much less research has been undertaken on the cache sites used by wild populations and the variables that may affect the decision making process. Theories of optimal foraging predict that animals should evolve foraging strategies that maximise their net energy gain (i.e. energy profit exceeds energetic loss during foraging) (MacArthur & Pianka 1966). Given that the fitness of the storer is influenced by whether or not caches are successfully retrieved, being able to prevent conspecifics and heterospecifics from pilfering your food is necessary for caching behaviour to remain adaptive (see Anderson & Krebs 1978; Smith & Reichman 1984). As a result, other researchers (including myself in this thesis) have sought to test the hypothesis that animals should not only make caches when economically sensible (i.e., energy return from caches outweighs cost of caches) but that such items are cached in sites that make it difficult for cache robbers.

The necessity of individuals to both create caches and then protect their cache sites became the foundation of my objectives in this thesis. The feeding experiments detailed in Chapter 2 are based on optimal foraging theory; namely, that animals should only cache when the net return of energy is greater than energy expended retrieving the cache. Animals should also take into account the likelihood of their cache being pilfered and time it takes to retrieve the cache that could have been spent doing other activities. Natural selection should thus favour those individuals that best weigh up these considerations. Several studies have demonstrated that food-hoarding rodents change their caching behaviour depending on the size of nuts and seeds they store, however, there is an absence of similar information on food caching birds. In Chapter 2, I demonstrated that New Zealand robins, a species that often caches for only a day also makes caching decisions based on the size of their prey. Robins usually consumed the first 5 to 10 mealworms fed at the beginning of trials, presumably to satiate their hunger. However, beyond the first 5 to 10 mealworms, robins almost always cached the largest mealworms, while the smallest mealworms were mostly eaten and very rarely cached. It appears robins use prey size as a cue for whether or not to cache food items. When foraging naturally for prey, robins are known to capture very large prey, such as native earthworms (Lumbricidae) and weta (Anostostomatidae) (Powlesland 1980). Often these prey are too big to eat intact and require breaking into smaller bits, some of which are then cached. Given that different sized bits would result, it would be advantageous for robins to be able to judge the size of food bits and eat the smallest and cache the largest. My experiment with different-sized mealworms confirms that prey size plays a role in the propensity of a robin to cache.

As with other caching birds, robins store prey for later when there may be a shortage of food or a long period of overnight fasting. Such a benefit might be lost

however, if the caches they create are then lost to pilferers. One might also expect more valuable prey (e.g. larger items) to be cached in safer locations to minimise the risk of pilfering. However, in my experiments in which I altered prey size, robins did not change the distance, height or time spent caching. These three variables are related and/or correlated to strategies used by other species to protect their cache sites. From my study it appears that robins do not go to more effort to protect more valuable cached food. I conclude that hiding larger food items further away does not appear to provide an increased benefit to robins because otherwise they would have evolved this strategy. One could argue that strategies to protect caches from pilfering are only expected to evolve if pilfering is in fact occurring. Robins regularly pilfer their mate's caches, and there is some evidence of pilfering of robin caches by other species (Steer 2006). Perhaps pilfering by a mate is accepted because it provides more important benefits, such as the success of fledging offspring. This cannot explain why pilfering by other species would be tolerated, but as the risk of this seems relatively low, at least from the little data available on the matter, that it may not have favoured a change in caching behaviour. Nevertheless, further data is needed on the rates of cache pilfering, by both mates and by other species.

If the risk of pilfering is high, natural selection should favour individuals with the best strategies for protecting their caches. Several studies have shown the various strategies used by scrub-jays and other corvids for protecting their caches and for pilfering the caches of other individuals. In Chapter 3, I demonstrated that robins react to pilfering in ways that I predicted and are supported by other research. The day after experimental pilfering occurred robins hid food further away from the feeding point and out of sight. Robins tended to cache higher up in trees after I experimentally pilfered their cache (though the data was not quite significant), which should help to place food further away

from any future pilferer. They also tended to eat more mealworms immediately; by doing so the food was immediately removed and robins did not risk the food being pilfered.

Finally, in Chapter 4 I found that robins did not appear to change their caching behaviour as a result of any of the attentional states tested. Although all the results were insignificant, there is much scope for future research (see below). However, robins did change their caching behaviour as a result of standing at different distances from the feeding point. Robins cached more food when I stood further away from the feeding circle. This can be explained by different distances representing different levels of threat. The closer to the feeding circle I stood, I predicted the greater threat I would pose to the robin and they would immediately eat more mealworms. Robins also tended to cache food further away from the feeding point, but this was not quite significant.

There appears to be common trends shown in Chapters 3 and 4 that robins cache food further away and eat food immediately rather than cache when the risk of pilfering and/or threat is greater. It is likely robins evolved these strategies to protect their caches from conspecifics. Considering robins employ these strategies in response to a human observer in what is a rather novel situation, it is likely that the response of robins to other robins would be even stronger because behaviours would have evolved specifically for this scenario. Although I am confident that these trends are real, caching further away in the distance experiment (Chapter 4) and food being eaten immediately in the experimental stealing experiment (Chapter 3) were not quite significant. Both had p-values close to 0.10. If the data set had a larger sample size I think results would approach significance. However the low number of robins at my study sites limited my ability to test further individuals during the course of the study, and it would be valuable to repeat this work

with other birds in this population (and other populations) to determine if the pattern I found are repeated.

5.2 Suggestions for future research

The caching behaviour of New Zealand robins has only recently started to be studied in detail (Powlesland 1980). There has been little research on the cognitive abilities of robins, such as, how many cache sites can be remembered, how they relocate caches or whether they use the gaze direction of other robins to choose their cache sites. There has also been no detailed comparative work on the three sub-species (or species depending on taxonomy used) of robins (North Island robin, South Island robin and Stewart Island robin) and we do not know if they differ behaviourally or cognitively. There has also been no work to know if robins respond differently to unfamiliar people and whether robins respond to human gestures in cooperative tasks, such as gestures towards a container that holds a food reward.

Alexander *et al.* (2005) suggest that some aspects of the food hoarding behaviour of North Island robins differed from that of South Island robins. First, they found North Island robins always cached mealworms whole; Powlesland (1980) found South Island robins dismember large prey prior to caching. In my study, mealworms were never dismembered at the feeding point and mealworms in caches were always whole. This is probably because mealworms don't grow to a size that they need to be dismembered. Second, Alexander *et al.* (2005) found North Island robins frequently cached several mealworms in cache sites whereas Powlesland (1980) found South Island robins rarely used the same cache site more than once and typically used different sites to cache separate

food items. South Island robins in my study sometimes cached in the same location and I suggest that the difference found between studies is because Alexander *et al.* (2005) fed a relatively large and concentrated source of mealworms to robins, whereas Powlesland (1980) reported on robins that were feeding on prey they naturally caught. Apart from these two differences between North and South Island robins, Alexander *et al.* (2005) suggest both species have similar food hoarding behaviours, but as no studies have directly compared the behaviour of North and South Island robins, this is a worthwhile area of research

Van Horik & Burns (2007) found that male North Island robins often use the same cache site as the last for the next worm they cache. They compared females with males and alone with mate present, although they found differences, robins tended to cache in the same site than caching in a different site. Their result is quite different to my study, where I found South Island robins almost always cached in a different site; the results were the same for both before and after pilfering. I conclude the robins in this study widely scatter their caches in response to a concentrated food source and most often do not hoard food in the same cache twice and very rarely in the same cache thrice. I observed that robins sometimes reused the same caches from day to day. It would make sense that some cache sites might appeal to robins more than others, such as one that provided a good look out for competitors or a site that does not provide a good lookout (if I cannot see them, then they cannot see me).

One of the difficulties in my study is that the number of birds present in my area was low, likely due to the high number of introduced mammalian predators. The density of robin populations varies greatly over New Zealand: predator free offshore islands often have very high densities whereas mainland forests have low densities of robins. It would

be interesting to know if robins change their caching behaviour depending on the density of conspecifics (and hence risk of pilfering). Unlike scatter-hoarding rodents that bury seeds within the soil, robins do not seem to go to any effort to hide their caches. Therefore, caches should be more conspicuous to pilferers but pilferers may be few and far between at mainland sites. Given the relatively low density of robins at my study sites in Kaikoura, there are probably relatively very few pilferers; this is because the total number of robins across the area is very low compared to predator free islands and because the robins have large territories, so overlapping home ranges between rival males may be small. At the nearby Waimangarara Forest, pest control has occurred for several years, and it appears that robins are found at higher densities than in the Kowhai Bush. Given this difference, it would be interesting to see if population density does affect pilfering frequency, and if this in turn alters the caching behaviours of the birds in each population. Similarly, it would be valuable to measure levels of pilfering on predator free islands and how this compares to that observed in mainland populations. Where densities are higher I predict robins are likely to change their caching behaviours to try and reduce pilfering.

Studies on caching have rarely looked at how cognition and behaviour changes with the ontogeny of animals (Bugnyar *et al.* 2007). In marsh tits, food storage begins at an early age but caching behaviours develop with experience and this is accompanied by developments in the region of the hippocampus (Clayton 1992; Clayton & Krebs 1995). Future research could look at how caching behaviour changes with the ontogeny of robins both between birds of different ages, and between the same birds in different years. It would be interesting to see if mature robins have an enlargement of the hippocampus compared to juveniles or related but non-caching robins in Australasia. In Kowhai Bush and Waimangarara Forest, many robins can be easily identified using colour bands, and the

age of birds that were banded as a fledgling is known. I also found very little information in the literature on how caching behaviour varies from year to year in response to changes in climate and food resources. Research has already looked at how the frequency of caching, pilfering and re-caching of male and female robins changes seasonally (Steer & Burns 2008). However, knowing how caching animals change their behaviour from a 'good' to a 'bad' year or wet to a dry year may provide insight into how caching animals in specific areas will respond to environmental change. Maybe caching animals will be better off than non-caching animals if food shortages are occurring more regularly.

Some caching animals are known to suffer high levels of cache loss (Baker & Anderson 1995; Stevens & Krebs 1986). Male and female robins are known to regularly pilfer each other caches but little has been documented on whether robins regularly pilfer caches of rival birds (Burns & van Horik 2007; van Horik & Burns 2007). Video data (180 minute tape) recorded immediately after caches were made shows caches were retrieved by rival birds as well as mates and the caching individuals themselves (C. Longbottom, personal communication). An issue raised in this study was that large bipedal mammals (humans) are probably quite conspicuous to robins and although cameras were set up several metres from the cache site, it is possible experimenters drew the attention of other robins to the area given that robins are generally quite easy to attract. Published research could look at the frequency of caches retrieved by these three groups.

5.3 Conclusions

This study emphasises the fact that robins make ideal species for behavioural research because they are exceptionally easy to observe in their natural environment. This cannot be

said for other birds used in caching research, which are often hand raised and tested in aviary/laboratory. Our current knowledge of caching behaviour in birds is mostly based upon previous research on Northern Hemisphere species. By demonstrating that robins can be manipulated in their natural environment and subsequently changing their behaviour, lays the groundwork for studying caching behaviour in wild populations of this species, and perhaps even lead to studies on the cognition of these birds in the wild. I suggest that New Zealand robins are an ideal Southern Hemisphere species to study caching behaviour. Overall, this research sheds light on an exciting area of animal behaviour with plenty of scope for more research.

5.4 Literature cited

Alexander, L., Duthie, C., Fyfe, J., Haws, Z., Hunt, S., Montoya, I., Ochoa, C., Siva, A., Stringer, L., van Horik, J. & Burns, K. C. 2005. An experimental evaluation of food hoarding by North Island robins (*Petroica australis longipes*). *Nortornis*, **52**, 138-142.

Andersson, M. & Krebs, J. 1978. On the evolution of hoarding behaviour. *Animal Behaviour*, **26**, 707-711.

Baker, M. C. & Anderson, P. 1995. Once-pilfered cache sites not avoided by black-capped chickadees. *Animal Behaviour*, **49**, 1599-1602.

Bugnyar, T., Stöwe, M. & Heinrich, B. 2007. The ontogeny of caching in ravens, *Corvus corax*. *Animal Behaviour*, **74**, 757-767.

Burns, K. C. & van Horik, J. 2007. Sexual differences in food re-caching by New Zealand robins *Petroica australis*. *Journal of Avian Biology*, **38**, 394-398.

Clayton, N. S. 1992. The ontogeny of food-storing and retrieval in marsh tits. *Behaviour*, **122**, 11-25.

Clayton, N. S. & Krebs, J. R. 1995. Memory in food-storing birds: from behaviour to brain. *Current Opinion in Neurobiology*, **5**, 149-154.

Clayton, N. S., Dally, J. M. & Emery, N. J. 2007. Social cognition by food-caching corvids. The western scrub-jay as a natural psychologist. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **362**, 507-522.

Cowie, R. J., Krebs, J. R. & Sherry, D. F. 1981. Food storing by marsh tits. *Animal Behaviour*, **29**, 1252-1259.

Dally, J. M., Emery, N. J. & Clayton, N. S. 2004. Cache protection strategies by western scrub-jays (*Aphelocoma californica*): hiding food in the shade. *Proceedings: Biological Sciences*, **271**, S387-S390.

Dally, J. M., Emery, N. J. & Clayton, N. S. 2005. Cache protection strategies by western scrub-jays, *Aphelocoma californica*: implications for social cognition. *Animal Behaviour*, **70**, 1251-1263.

Dally, J. M., Clayton, N. S. & Emery, N. J. 2006. The behaviour and evolution of cache protection and pilferage. *Animal Behaviour*, **72**, 13-23.

James, P. C. & Verbeek, N. A. M. 1983. The food storage behaviour of the northwestern crow. *Behaviour*, **85**, 276-291.

MacArthur, R. H. & Pianka, E. R. 1966. On optimal use of a patchy environment. *The American Naturalist*, **100**, 603-609.

Powlesland, R. G. 1980. Food storing behaviour of the South Island robin. *Mauri Ora*, **8**, 11-20.

Roberts, R. C. 1979. The evolution of avian food-storing behavior. *The American Naturalist*, **114**, 418-438.

Sherry, D., Avery, M. & Stevens, A. 1982. The spacing of stored food by marsh tits. *Zeitschrift für Tierpsychologie*, **58**, 153-162.

Smith, C. C. & Reichman, O. J. 1984. The evolution of food caching by birds and mammals. *Annual Review of Ecology and Systematics*, **15**, 329-351.

Steer, J. 2006. Seasonality of food use and caching in New Zealand robins (*Petroica australis*). MSc thesis, Victoria, University of Wellington.

Steer, J. & Burns, K. C. 2008. Seasonal variation in male-female competition, cooperation and selfish hoarding in a monogamous songbird. *Behavioral Ecology and Sociobiology*, **62**, 1175-1183.

Stevens, T. A. & Krebs, J. R. 1986. Retrieval of stored seeds by marsh tits *Parus palustris* in the field. *Ibis*, **128**, 513-525.

van Horik, J. & Burns, K. C. 2007. Cache spacing patterns and reciprocal cache theft in New Zealand robins. *Animal Behaviour*, **73**, 1043-1049.

6.1 Acknowledgements

I want to start by thanking my supervisor, Jim Briskie, his advice and wealth of knowledge helped me in the experimental, theoretical and writing up stages of this thesis. I would also like to thank my associate supervisor, Ximena Nelson for her support and knowledge about statistics.

I undertook my research in Kaikoura, where I had assistance from a number of people including Mailee Stanbury, Leslie Poulson, Miles Burford, Brian Thorne and Chris May. Thanks to Rennie Bishop for cutting the tracks in Kowhai Bush and providing the hundreds of mealworms I required. Many thanks to Barry and Jenny Dunnet for their knowledge of Waimangarara Forest, cutting the tracks and setting up a system of bait stations and kill traps. Thanks to Jack van Berkel for my accommodation at the Kaikoura field station.

Finally, thanks to my family, friends and especially my parents Kathleen and Gary Tibble. It is because of your support for the last two years that this journey has been so pleasurable.